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BOTANICAL NOTES ON THE CANARY ISLANDS
II. THE EVOLUTION OF PLANT FORMS IN THE ISLANDS: AEONIUM

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Introduction

Botanists interested in evolution have for some time cast envious glances in the direction of Darwin's finches. This group of birds is now popular with textbook and magazine writers as an example of evolution in ecological and geographic isolation. Lack (1947) has demonstrated that the habits and habitats of these finches have undergone evolutionary changes in the Galápagos and neighboring islands, resulting in many species which can be distinguished by their adaptation to various ways of life, their adjustments to certain feeding habits, and other features of ecological significance.

Among the flowering plants it has been difficult to find as illustrative a group of species whose evolution could be attributed so precisely to certain selective forces and ecological functions. In fact, the important botanical contributions to evolution have been made in the area of genetic mechanisms (polyploidy, introgression, changes in chromosome composition, and other sources of variability) rather than in the field of natural selection of differently adapted types.

The fossil record of flowering plants is so fragmentary that it fails to point to any type as ancestral. We hear statements that angiosperm trees are more ancient than shrubs and herbs (Hansen 1956), that annuals are derived rather than primitive. Corroboration of these notions has come primarily from studies of vascular anatomy (Bailey 1944); but information about the precise changes in morphology, and the ecological factors which might have led to the evolution of herbs from shrubs, or annuals from perennials is indeed scarce.

In this paper I shall demonstrate ecological evolution among a group of plants centered in the Canary Islands. As I shall discuss in some detail, this group is composed of species of many forms from shrub to biennial and annual herb; it is possible to derive all of them from a shrubby ancestor, to show what changes in morphology have occurred and what ecological factors might be behind these changes. I believe that we are dealing with a situation comparable in many ways to the finches of the Galápagos, one with great potential for detailed cytological, genetic, and anatomical investigation.

Acknowledgments

The following account of the Sempervivum group in the Canary Islands is based upon field work in these islands during the summers of 1954 and 1956. These travels were made possible by Prof. H. H. Bartlett, former director of the Botanical Gardens of the University of Michigan, and Prof. A. G. Norman, his successor. Without sponsorship by their institution this project could not have materialized, and I am truly grateful for this help. Living plants were cared for in the Botanical Gardens by W. F. Kleinschmidt and his staff, who helped greatly in this way.

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Origin of the Canarian Sempervivum Flora

Distribution of the taxa

R. Lloyd Praeger, renowned botanist of Ireland, did not limit his talents to that country: after years of botanical exploration abroad he wrote a monograph on his favorite plants, the Sempervivum group (1932). He recognized five genera, including Sempervivum itself ("Houseleeks" of the European mountains) and Aeonium (shrubs and subshrubs of the Atlantic islands and Africa), Greenovia (rosette plants of the Canary Islands), Aichryson (annuals of the Atlantic islands) and Monanthes (dwarf plants of the Canaries). These five genera, sometimes conceived as two or three only, make up the subfamily Sempervivoideae of the Crassulaceae (Stonecrop family). The members of this family are almost all xeromorphic, with succulent leaves and stems; Praeger's Sempervivums are no exception.

Figure 1 shows that most species of Aeonium, Aichryson, Greenovia and Monanthes are peculiar to the Canaries. Here they occupy almost every available habitat except the very dry desert slopes to the South. Outlying stations like the African coast, Madeira, the Cape Verde Islands and the Azores have so few species that we may regard the Canary Islands as the center of speciation in this group of plants. The first problem with which we are confronted is: from where did the ancestors of these plants come and when did they arrive?

Geographic elements

Schmid (1954) furnishes a list of geographic elements in the flora of the Canary Islands which recognizes different times of arrival for the several floristic groups, an inference not readily drawn from earlier classifications (Pitard and Proust 1908). Schmid includes recent invaders from the Sahara (*Launaea spinosa, Tamarix* spp., Phoenix), members of several Mediterranean floristic groups (Juniperus, Cistus, Erica, Cytisus), representatives of a temperate rainforest, extinct since the Pliocene (cf. Depape, 1922) except for fragments on the Atlantic islands (Persea, Ocotea, Myrsine, Notelaea), and finally members of even older, fragmentary floras which have become disrupted geographically as a result of climatic changes.

Prominent among these disjuncts are the members of an "ancient African" semidesert flora (term coined by Christ 1892), now scattered in the mountains of South and East Africa, on Socotra, on the Atlantic islands, and occasionally the coast of Morocco. This interesting pattern of distribution is seen in Euphorbia (the cactoid *E. canariensis* and *E. handiensis,* and the group of *E. regis-jubae*); also in Kleinia (S. African Composite genus with *K. neriifolia* in the Canaries and *K. anteuphorbium* in Morocco) and a host of others. One disjunct species of Aeonium (*A. leucoblepharum* or *A. chrysanthum*) occurs in Abyssinia, Eritrea and S. W. Arabia (Fig. 1). This species, a member of the primitive section Holochrysa (see page 5), constitutes the only link between the Sempervivum group and the East and South African center of the Crassulaceae. It places the genus Aeonium among the older members of the Canary Island flora.

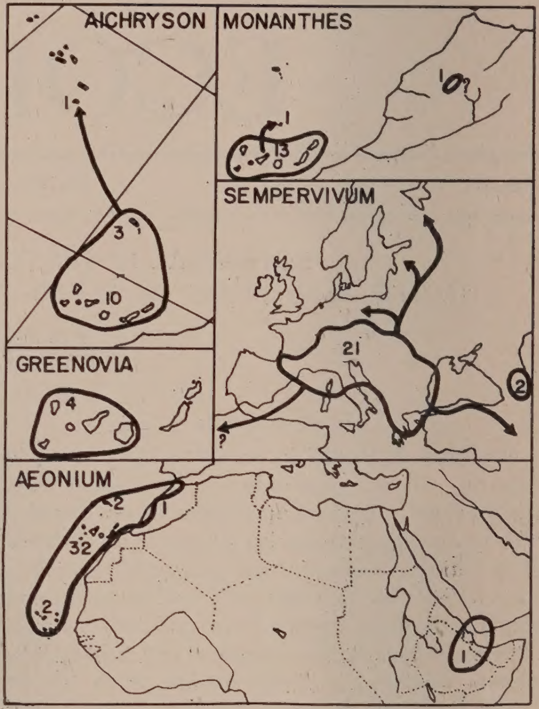

Fig. 1. Distribution of the genera of the Sempervivum group. Numbers of species are indicated. Outlying stations are indicated by arrows.

Climatic considerations

Although the Sempervivum group is xeromorphic, none of the species has survived the drying climate in the Sahara. To this day most species of Aeonium require atmospheric moisture and thrive best on slopes exposed to the trade wind from the Northeast. The Aeoniums must at one time have been more widely distributed across North Africa, together with species of Kleinia, Euphorbia and other members of that old semidesert flora. How else can the present disjunct distribution of these plants be explained?

To answer the question of the age of Aeonium as an Atlantic group of plants we need to know more about the age of the Sahara as a dry desert. According to Gautier (1935) this region has been desert-like at various times, going back as far as the Silurian. These dry eras alternated with pluvial periods, the most recent of which occurred in the Pleistocene. But this wet period was limited in its extent over the Sahara, and it is doubtful that so many species could have evolved following a migration during the Pleistocene. There, are, however, fossil river beds and basins in the Sahara attributed by Gautier to another, more extensive rainy climatic era, which most authorities place in pre-Pliocene times; some even consider it Oligocene. We may suppose, then, that during the latter half of the Tertiary, climatic deterioration broke up the range of certain plant populations across the Sahara. At that time many populations found refuge in the Atlantic islands, where a greater stability of climate prevails.

In thinking about evolution on islands, I find two climatic features of importance: diversity and stability. Only in areas with great climatic diversity is evolution likely to produce the wealth of forms which we encounter in the Canary Islands. It is this climatic diversity which is largely responsible for swarms of young endemics on islands.

In the Canary Islands the variety of climatic types is due to the great elevation of several islands (3,711 m. for Tenerife), causing fog and rain to precipitate between 300 and 1500 m. The north and east slopes, being exposed to the trade wind during most of the year (the latitude is 28°N.), provide further contrast with the arid southerly exposures. Some climographs are presented in Figure 2, along with those of nearby continental localities.

The climatic stability referred to above is insured on the one hand by the surrounding ocean which tends to buffer the temperature and the humidity of the air, and on the other hand by the elevation of the islands, intercepting this humidity at a certain altitude. This type of stability has favored the survival of ancient forms of plants (*Dracaena draco,* Echium sect. Simplicia, Sonchus sect. Dendrosonchus, Bencomia and its allies, etc.). Climatic stability and diversity are not mutually exclusive, and on mountainous islands such as the Canaries a combination of the two has resulted in the proliferation of youthful endemics derived from ancient survivor populations, some of which have retained remarkable genetic plasticity.

Historic factors

The islands are further suitable as a refugium because they are geologically old, certainly of mesozoic age (Hausen 1956). The seven major islands are Lanzarote, Fuerteventura, Gran Canaria, Tenerife, Gomera, La Palma, and Hierro. They are the summits of a system of volcanoes which arose beyond the edge of the African land mass, perhaps at a time when tectonic stress was shaping the chains of the Atlas Mountains (this relationship would explain the SW—NE orientation of the rows of islands). There is no evidence, either in the nature of their rock, or in the depth of the ocean surrounding them, that the Canary Islands were ever connected by land with Africa. Their small flora (about 1450 vascular plants, including the naturalized weeds), and the fragmentary fauna (no mammals, no snakes) confirm this idea.

There has been no wholesale invasion of aggressive Mediterranean plants. Only species with long-range dispersal mechanisms were established spontaneously (e.g. the berry producing *Juniperus phoenicea, Pistacia lentiscus, Olea europaea,* even *Phillyrea angustifolia;* but not their associates, *Quercus ilex, Chamaerops humilis,* with heavier fruit). In recent times man's weeds have begun to appear on the scene, encouraged by land use and irrigation.

Summary

The genus Aeonium reached the Canary Islands from the Moroccan coast at a time when the ancestral population was widespread. In view of the age of the Sahara desert this may have happened during the first half of the Tertiary, if not earlier. We shall now see how this group has evolved in the variety of habitats available in the Canary Islands.

Taxonomy and Growth Forms of the Sempervivum Group

Growth forms

The concept of growth form as it is used here is inspired by earlier works on shoot morphology (Warming 1908), stem types and branching patterns (Du Rietz 1931). The term *life form* is not used in this paper because it should be reserved for the relationship between renewal buds and soil level, as formulated by Raunkiaer (1934). The term *growth form* refers to the development and architecture of the shoot system and its appendages, including the arrangement and periodicity of the leaves, and growth patterns of vegetative and reproductive branches.

Although not widely recognized as such, the works of Schimper (1903), Raunkiaer (1934) and Warming (1908) on the statistical incidence of different plant forms in different climatic and vegetational provinces are really the foundation for studies of evolution in the Angiosperms. More recently Dansereau (1952) has provided an hierarchic system of the major vegetational formations and their governing climatic factors,

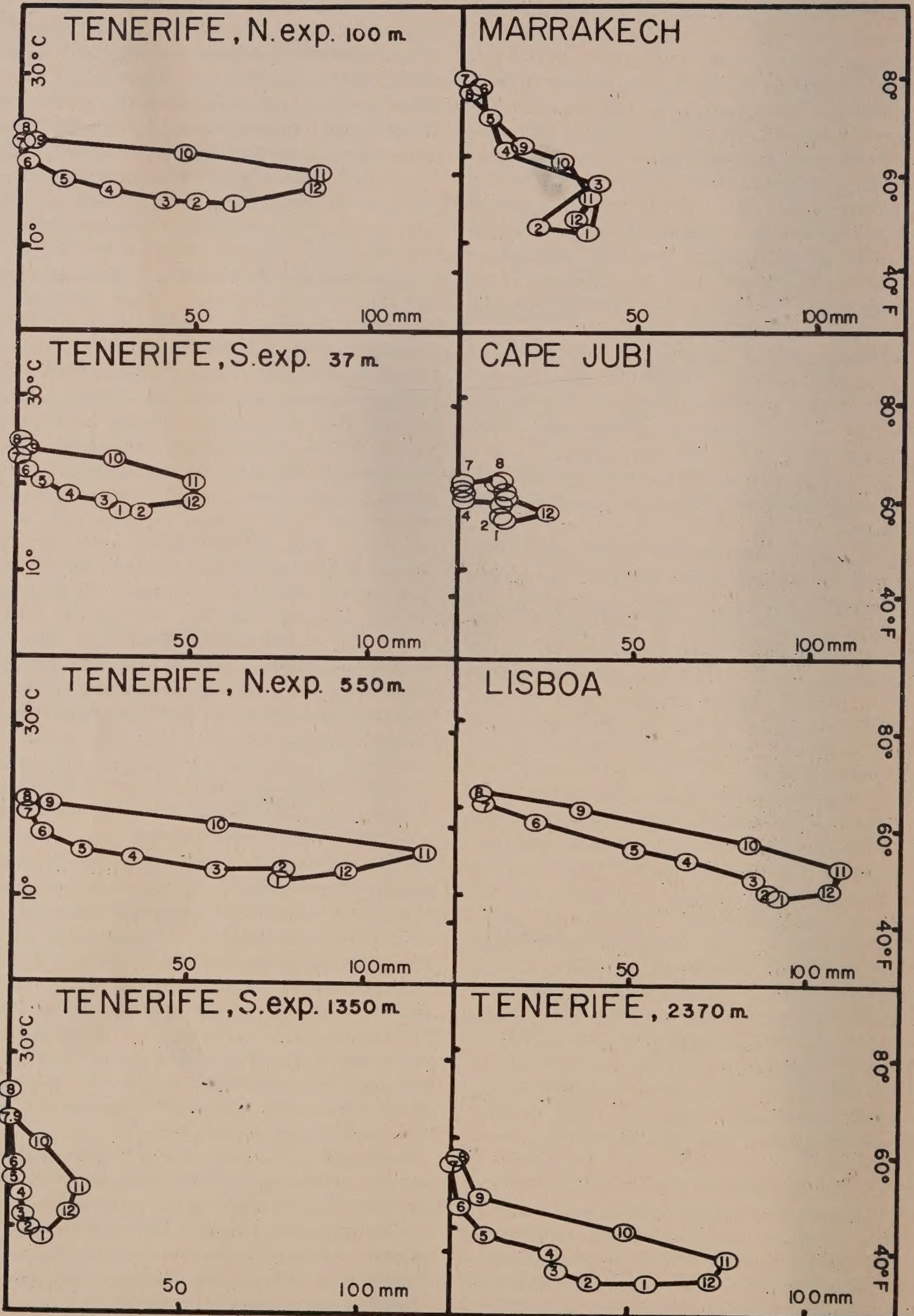

FIG. 2. Climographs of several elevations and exposures on Tenerife, compared with climographs of Morocco and Portugal.

TABLE I. Characteristics of the sections of *Aeonium, Aichryson* and *Greenovia*

Section or genus: (Praeger, 1932)	Synonyms (Berger, 1930)	Petal color	Petal number	Leaf margin	Number of species:	Growth forms:
Holochrysa	Euaeonium	yellow	8-12	ciliate	9	crassicaulous shrubs, monocarpic shrubs
Megalonium	Megalonium	dark red	7- 8	entire	1	monocarpic shrub
Urbica	Leuconium	white or pink[1]	6- 9	cilia or cartilaginous teeth	11	crassicaulous or woody shrubs or subshrubs, candelabrum plants and monocarpic shrubs
Canariensia	Pittonium Patinaria	yellow	7-13	ciliate	8	rosette plants, branched or monocarpic
Goochia	Auonium Trichonium Anodontonium p.p.	yellow[1]	7-16	ciliate or entire	9	dwarf shrubs, stoloniferous rosette plant
Aichryson	Anodontonium p.p. Aichryson	yellow	5-12	entire or punctate	13	annuals, short-lived dwarf shrubs
Greenovia	Greenovia	yellow	20-32	entire, hyaline	4	rosette plants, monocarpic or stoloniferous

[1] With one or two exceptions.

and redefined each formation in precise structural terms (1958). Thus, the background and tools for a study in ecological evolution are close at hand.

Since the days of Warming and Raunkiaer the study of plant growth forms has been neglected in favor of plant sociology and ecology on the one hand, biosystematics and cytotaxonomy on the other hand. At the present time a revival of interest in plant forms occurs in Europe (Schmid 1956, 1957; Meusel 1951, 1952). In addition, our knowledge of fields related to the evolution of plant forms has been greatly enlarged: problems of variability and distribution of plant populations have gained in clarity from the works of Stebbins (1950), Clausen (1951) and numerous others. Plant anatomists and developmental biologists have reopened the discussion about the nature of the shoot apex (Plantefol 1947; Gifford 1954), and problems of shoot morphology are again being given attention.

With this account of growth forms in the Sempervivum group I hope to attract the attention of both systematists and morphologists. It would be pleasing indeed to have the developmental and evolutionary mechanisms of these plants worked out in detail, since they present such an excellent example of adaptive radiation with their wide variety of forms. This discussion will center around the latter phenomenon and its causes.

Taxonomy

Two monographs are at hand, one by Praeger (1932), one by Berger (1930), both of whom divide the genus into several sections. The best collection of photographs of the plants in their natural setting is presented by Burchard (1929).

For all its variety of growth forms, the Sempervivum group is very uniform in floral morphology. Only number and color of petals are variable, even within the species; occasionally the shape of certain floral scales is helpful. The monographers have frequently found it necessary to resort to leaf shape, leaf margin and growth form for the distinction of major divisions within the genus Aeonium. Even alleged genera like Aichryson offer little to set them apart besides the fact that they are annuals.

Table I reviews the subdivisions of the Sempervivum group and some of their characteristics. In my account of the growth forms I shall use Praeger's names which appear to have priority in most cases (1928), and seem less artificial. With the subdivisions in Table I there are listed a number of general growth forms. My observations on these forms, discussed below, are based upon specimens studied in the field, the herbarium, and in the greenhouse, where I watched the development of 16 species for more than four years. I found that these plants, introduced in 1954 and 1956 as cuttings or young plants, retain their branching patterns quite faithfully; although the leaf sizes may change somewhat, the general character of the plants is not modified and appears to be genetically fixed.

The section Holochrysa.—The Holochrysa are shrubs about 1 m high with thick, succulent branches. *Aeonium manriqueorum* of Gran Canaria, when grown in the greenhouse, branched regularly every year as long as the main axis remained vegetative. After three years the apical meristem became reproductive and terminated the growth of the main trunk with a large inflorescence. The next year the oldest lateral branch

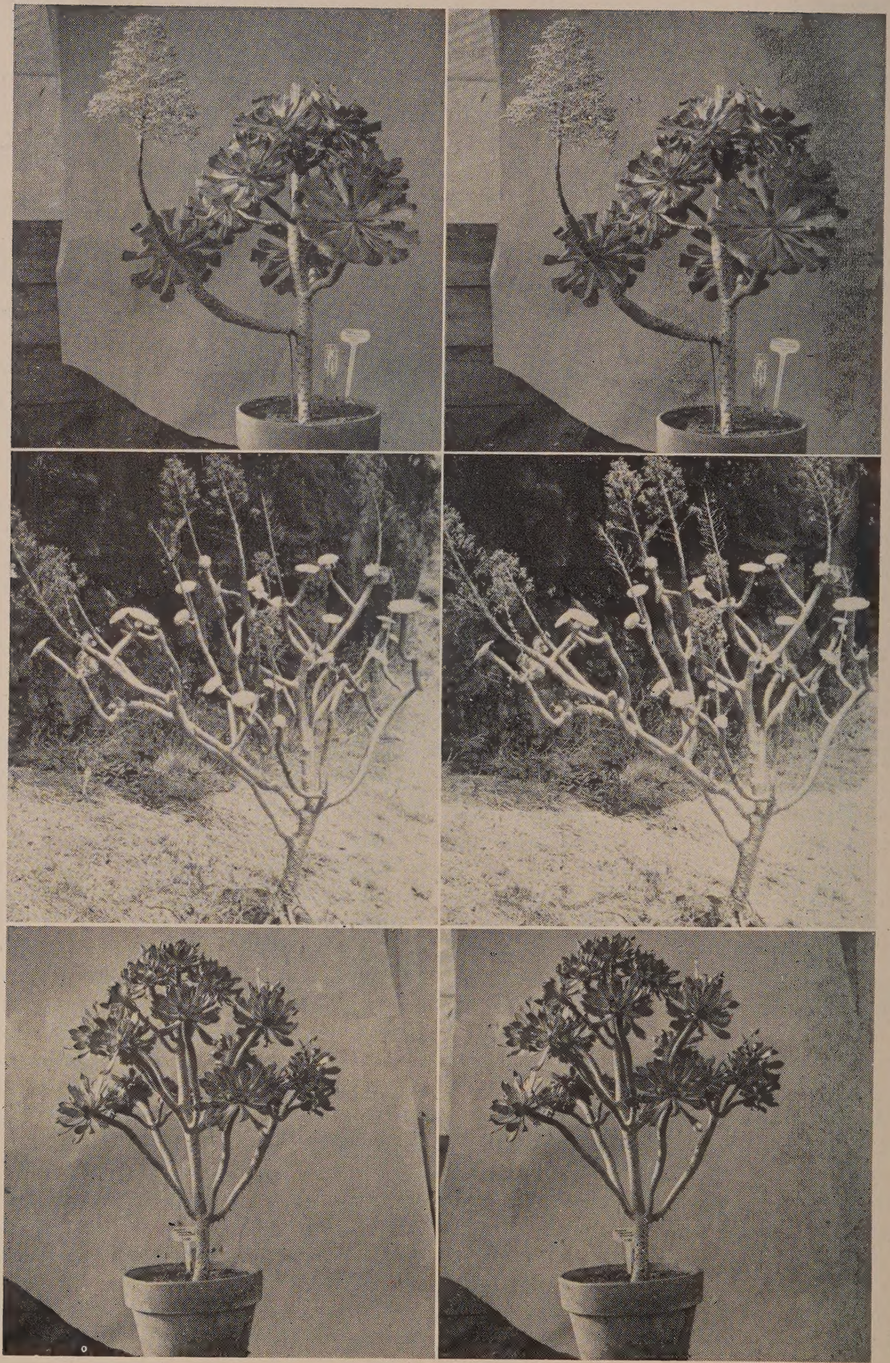

FIG. 3. Growth forms of Aeonium, section Holochrysa.[1] Top pair: *A. manriqueorum* of Gran Canaria, 4 yrs. old, flowering second year. Middle: *A. holochrysum,* shrub in summer condition, about 12 yrs. old. Note old inflorescences and small rosettes of leaves. La Palma, 1956. Bottom: *A. arboreum,* about 3 yrs. old. Note adventitious roots.

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[1] Stereo pairs may be viewed through commercial viewer or with two reading glasses, oriented properly.

turned reproductive (Fig. 3,* top). The inflorescences eventually dried and fell off, leaving ugly stumps. Lateral shoots had meanwhile taken over. The same type of determinate growth occurs in *A. holochrysum* (Fig. 3, middle), and most other Holochrysa, e.g. *A. arboreum* (Fig. 3, bottom).

In the Canaries the Aeoniums of this type are most commonly associated with other thick-stemmed plants of African affinity growing in the coastal areas below the cloud belt. Here the vegetation is dominated by associations of *Euphorbia regis-jubae, Kleinia neriifolia* and *Euphorbia canariensis.* This alliance is most common on dry, loamy slopes to the North and East, where the trade wind brings in humid air.

Aeonium webbii and *A. undulatum* present a difference in growth form. *Aeonium webbii,* an endemic of the Cape Verde Islands, grows up to almost 1 m without forming lateral branches. An enormous inflorescence terminates the unbranched trunk after many years, whereupon the plant dies (Berger 1930). It is, in other words, monocarpic.

Aeonium undulatum of Gran Canaria develops in much the same way. However, certain buds on the stem below soil level sprout forth and form new monocarpic stems (Praeger 1932). The life of the individual is thus "saved" by branching from the base.

The section Megalonium.—*Aeonium nobile,* the strange monotype of this group, produces great succulent leaves of a bright orange hue, and a large inflorescence with dark red flowers. The growth form is again monocarpic: for ten or fifteen years the plant consists of a rosette of leaves on a thick stem, finally several decimeters high. Then the shoot apex becomes reproductive and produces flowering branches. The plant dies after fruiting. Praeger, who discovered this plant on La Palma, calculated that perhaps 500,000 seeds can be produced by a single inflorescence.

I saw this plant only on the oldest rock formations of La Palma, from near sea level to about 800 m, usually in soil pockets and crevices. It is accompanied by *Eurhorbia regis-jubae, Kleinia neriifolia,* and shrubs of *Echium leucophaeum,* all Canarian endemics.

The section Urbica.—The members of this section, characterized by glaucous leaves, occur in the warm coastal regions as well as higher in the mountains, where fog and rain are frequent. In most species the pattern of development is similar to that of the Holochrysa. Differences within this section are largely a matter of size and thickness of the shoots.

The first of four arbitrary categories is illustrated by *A. percarneum,* an endemic of Gran Canaria (Fig. 4, top), where it accompanies *A. manriqueorum* in the coastal belt. It grows to a height of about 7 dm with very fleshy branches and tight spirals of leaf scars. The inflorescence is umbrella-shaped with thousands of flowers (Fig. 4, second row). Grown in the greenhouse, this plant behaved much like *A. manriqueorum* but took more than four years to produce an inflorescence.

A second group of the Urbica is found primarily in the cloud belt. *A. ciliatum,* a common species of Tenerife, can be called a candelabrum plant: its low, lateral branches arch upward, supported by adventitious roots which become woody and thick (Fig. 4, 3rd pair). The plant may extend its vegetative branching system to form a sprawling bush, with large, long-stalked inflorescences (Fig. 5, top left). However, in nature where the plants grow in rocky openings and along the crests in the laurel forest they rarely have an opportunity to develop freely. They are accompanied by other ancient Canarian endemics (*Bencomia caudata, Chrysanthemum broussonetii, Sonchus abbreviatus, Aeonium cuneatum*), but are almost overrun by the aggressive tree heathers (*Erica arborea, Erica scoparia* ssp. *platycodon*) and the broadleaf-evergreens (*Laurus canariensis, Myrica faya*) which form a strange tension zone between the laurel forest, the tree heath and relics of much more ancient vegetation types.

The third growth form of the Urbica, the dense subshrubs, may be found in more arid situations. *Aeonium castello-paivae* of Gomera and *A. haworthii* of Tenerife are twiggy bushes, half a meter high, with thin, woody branches. The tips of the twigs with their bud-like leaf rosettes form a dense hemispherical mass (Fig. 4, bottom). These plants are the most xeromorphic among the Urbica.

Finally, there is the monocarpic type. In *Aeonium urbicum* (Fig. 5, middle left) and *A. hierrense,* occasionally even in *A. ciliatum* (Praeger 1932), lateral shoots fail to develop, so that the life of the plant ends with the production of the inflorescence. These monocarpic species grow in the coastal belt and in the lower cloud zone, generally in soil or in small pockets of soil in cliffs.

The section Canariensia.—Clinging to walls of rock, often covering them with masses of large rosettes, the members of the section Canariensia are the most conspicuous among the Aeoniums of

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* Stereopairs in this paper are not published at ESA expense.

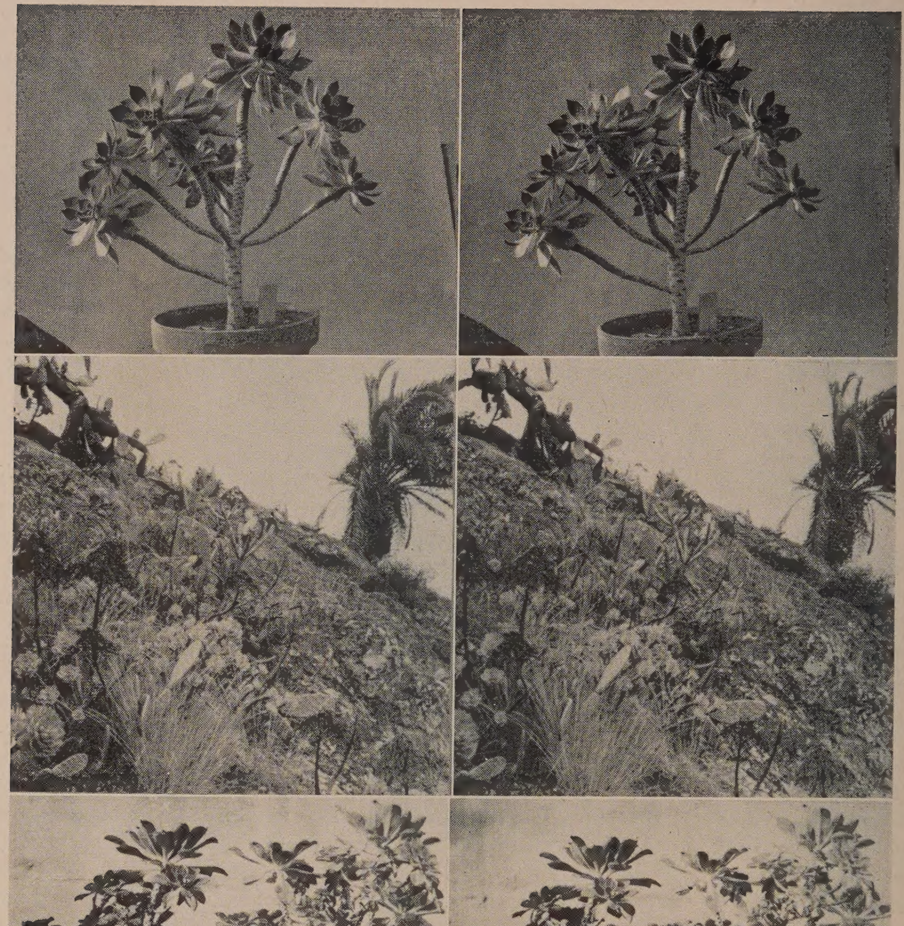


FIG. 4. Growth forms of the Urbica. Top pair: *Aeonium percarneum* of Gran Canaria, from 3 yr. old cutting. Second pair: rocky slope near Tafira, Gran Canaria, habitat of *A. percarneum* (note large fruiting inflorescences). Also showing *Aristida adscensionis, Kleinia neriifolia* (center), *Opuntia ficus-indica* (naturalized), *Phoenix canariensis.* Third pair: *Aeonium ciliatum,* 5 yrs. old, after first flowering shoot broke off. Cf. Fig. 6. Bottom pair: old specimen of *A. haworthiii.*

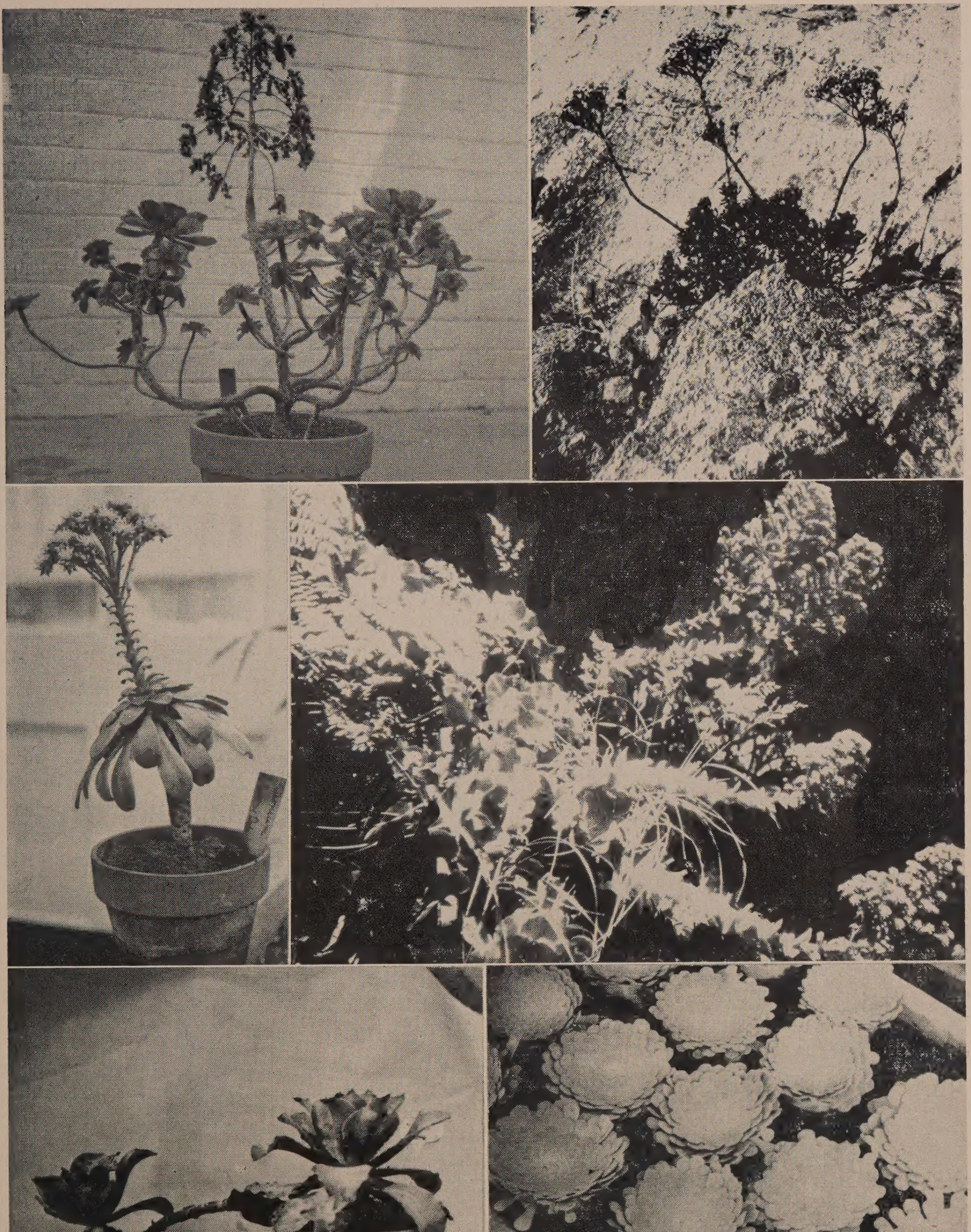


FIG. 5. Top left: *Aeonium ciliatum*, same plant as fig. 4. Top right: *A. spathulatum* in the subalpine of Tenerife. Middle left: *A. urbicum*, monocarpic dwarf shrub, 3 yrs. Middle right: *A. cuneatum* covering densely vegetated boulder in the laurel forest. Note rosettes and large inflorescences. Also shown: *Dryopteris filix-mas* ssp. *oligodonta*, *Agrostis* cf. *canariensis*. Bottom left: *A. cuneatum* with stolon. Bottom right: *A. tabulaeforme*, 2 yrs. old.

the islands. These rosettes may be produced on long stolons, as in *A. cuneatum.* The species is restricted to the laurel forests of Tenerife, where it covers mossy boulders with rosettes of glaucous leaves. These are produced on prostrate laterals from the lower part of the main stem (Fig. 5, bottom left). Some of these laterals produce inflorescences of golden-yellow flowers (Fig. 5, middle right), while others remain vegetative and give rise to new laterals.

Aeonium canariense and its close relatives, *A. palmense, A. virgineum,* and *A. subplanum* (insular races of the same species complex) are all sessile rosettes with scarcely woody stems. There are few lateral branches, and they are so short that dense clusters of rosettes are produced, from which the yellow inflorescences arise.

Two species of the Canariensia are monocarpic, and at the same time sessile rosette forms: *Aeonium tabulaeforme* of the North coast of Tenerife is a monocarpic rosette sprouting from crevices in cliffs, in the company of a few lichens and annual weeds (Fig. 6, second row). When grown in the greenhouse this plant remains flat or platter-shaped for several years (Fig. 5, bottom right) and dies after the production of a lax inflorescence. Its adaptation to living in crevices of steep rock walls is rather obvious.

Aeonium glandulosum is an endemic of the North coast of Madeira; it develops in the same manner as *A. tabulaeforme* of Tenerife, only in the span of two years as a biennial rosette plant. Both species are herbaceous.

The section Goochia.—All members of this group are much smaller than the Aeoniums previously mentioned, with much branched, twiggy vegetative bodies.

There is a great array of ecological forms within this section. The least specialized are the species of the humid north coasts of several islands: *Aeonium goochiae* of La Palma, *A. viscatum* of Gomera and *A. lindleyi* of Tenerife. They grow in cliffs and rocky soil, and have a tendency to hang down in long tresses.

Aeonium sedifolium and *A. saundersii* are narrow endemics of highly specialized habit. They grow out of crevices, at times elongating rapidly and branching out; then undergoing a summer rest period during which the leaves form rounded bud-like structures. *A. saundersii* grows only in two valleys of Gomera where I found it accompanied by small rock plants (*Micromeria densiflora,* mosses); its long twiggy stems sprawl over the rocks, sending down adventitious roots here and there.

Another highly xeromorphic form is *Aeonium spathulatum,* a dwarf plant of the dry subalpine region of Tenerife (above 1800 m.). This plant differs in growth habit in that the vegetative branches form a compact mass; the inflorescences protrude on long stalks from the vegetative body (Fig. 5, top right).

The only sessile rosette plant in the section Goochia is *Aeonium caespitosum* of the subalpine of Gran Canaria. It has axillary stolons, while the main stem becomes a corm-like organ, wedged in a crevice. I collected it in the company of *Greenovia aurea* and *Sonchus platylepis,* all subalpine rock plants.

The genus Aichryson.—About 13 species of the Sempervivum group have been placed in the genus Aichryson. They are hygrophytic annuals or biennials of moist and slimy soil along springs and brooks (Fig. 5, third row), especially common in the laurel forest belt. Some species are actually perennial dwarf shrubs (*A. tortuosum, A. bethencourtianum*) which link the genus Aichryson to the section Goochia of Aeonium. They suggest an evolutionary relationship between the two genera.

The genus Greenovia.—The four species of Greenovia are all endemic to the Canary Islands. They differ in several respects from Aeonium: shape of the placenta (Berger 1930), larger number of petals, and beaker-shaped rosettes of leaves on short stolons. The most common species, *G. aurea,* grows on rocks in the pine region (1000-2000 m.) on several islands, but always on rocky surfaces (Fig. 6, bottom). Clusters of thin stolons are formed. Flowers are borne on the original axis. *G. diplocycla* of La Palma is monocarpic, producing no stolons and flowering within three or four years.

In growth form these plants correspond closely to the section Canariensia of *Aeonium.* Although their origin is obscure, they are perhaps related to this group.

DISCUSSION

Primitive and derived growth forms

There is no doubt that the Canary Islands are the center of evolution of Aeonium. The species surviving there today must all be derived from a common ancestral population. Which of the contemporary forms, if any, resemble the ancestral type in their growth habit? Is it possible to designate among the array of growth forms which I have discussed those which are advanced or modified and those which are primitive?

In Figure 7 the growth forms are arranged to indicate a number of possible sequences. The

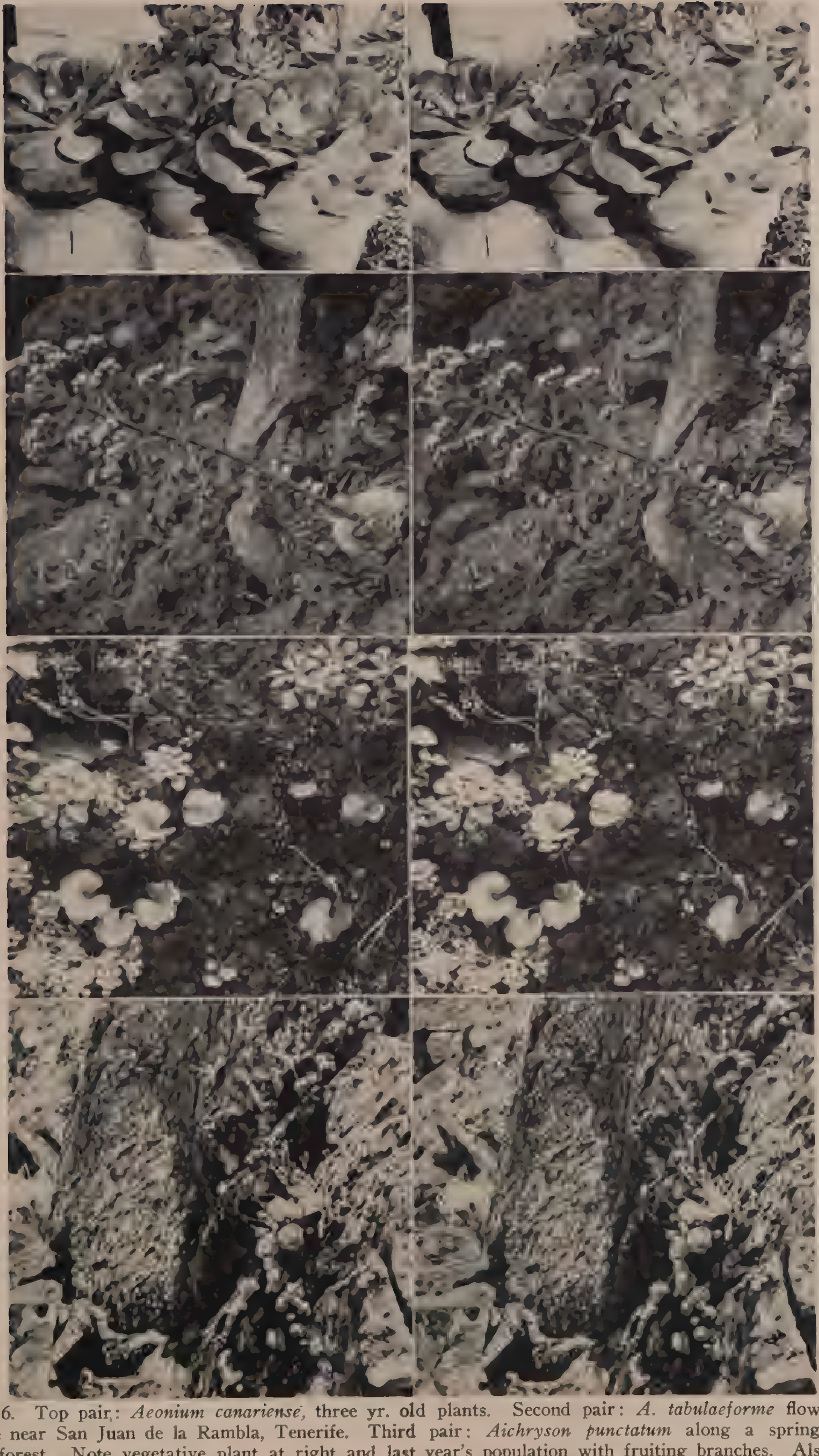
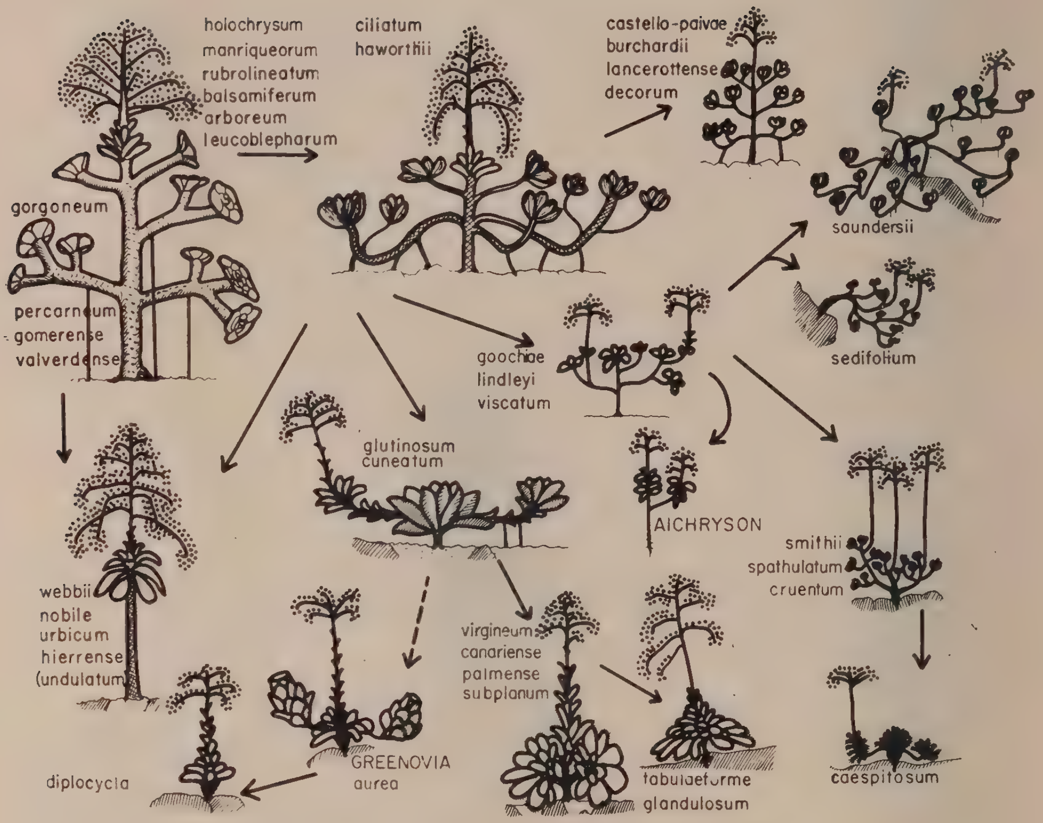


FIG. 6. Top pair: *Aeonium canariense*, three yr. old plants. Second pair: *A. tabulaeforme* flowering in a niche near San Juan de la Rambla, Tenerife. Third pair: *Aichryson punctatum* along a spring in the laurel forest. Note vegetative plant at right and last year's population with fruiting branches. Also showing: *Ranunculus cortusaefolius*, *Selaginella denticulata*, *Agrostis* sp., *Senecio lacteus*. Tenerife. Bottom pair: *Greenovia aurea* on Gran Canaria, accompanied by *Tolpis lagopoda* and *Leucophae candicans* (far background).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balsamiferum
arboreum
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ciliatum
haworthii
castello-paivae
burchardii
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canariense
palmense
subplanum
GREENOVIA
aurea
diplocycla
tabulaeforme
glandulosum
caespitosum

FIG. 7. The growth forms of the Sempervivum group, arranged in possible evolutionary sequences. Arrows do not indicate ancestral relationships between species, but rather morphological affinity.

arrows connect those types which might be derived from one another through a minimum of morphological change in the shoot systems. In this synthesis several criteria were used more or less independently, but all of them tend to confirm the same sequences. They are the following:

1. Characteristics of the vegetative shoot.
   a. Woodiness of the axis (Fig. 8 G). Schmid (1956) proposes a useful set of categories based on the degree of lignification of the axis, which is directly applicable to Aeonium. Most of the tall species (Holochrysa) are hemixylic (with small lignified core), but some of the dense, xeromorphic bushes have holoxylic stems, while many of the rosette plants of the Canariensia have oligoxylic stems (scarcely lignified).
   b. Length of the vegetative shoot (Fig. 8 A). Within the Sempervivum group the length of the shoot ranges from several decimeters (in the Holochrysa) to very short branches, making the vegetative plant practically sessile (in the Canariensia). Within a group such as the Urbica, the species can be graded according to this criterion.
2. Branching patterns.
   a. The number of lateral shoots produced (Fig. 8 B). In *Aeonium* the number of laterals shows an extreme range of variation, from completely unbranched (in the tall and low monocarpic species, evolved independently in the Holochrysa, Urbica, Megalonium, the Canariensia, and the genera *Aichryson* and *Greenovia*) to densely and continuously branching shoots such as one finds in the xeromorphic Urbica.
   b. The level at which the lateral branches are produced (Fig. 8 C) has a profound influence upon the fate of the plant. In those species of the Holochrysa which branch well above the ground, the single trunk must support a more and more elaborate mass of branches. In species with low and spreading laterals, the adventitious roots may help the spread of the plants. This tendency appears inde-

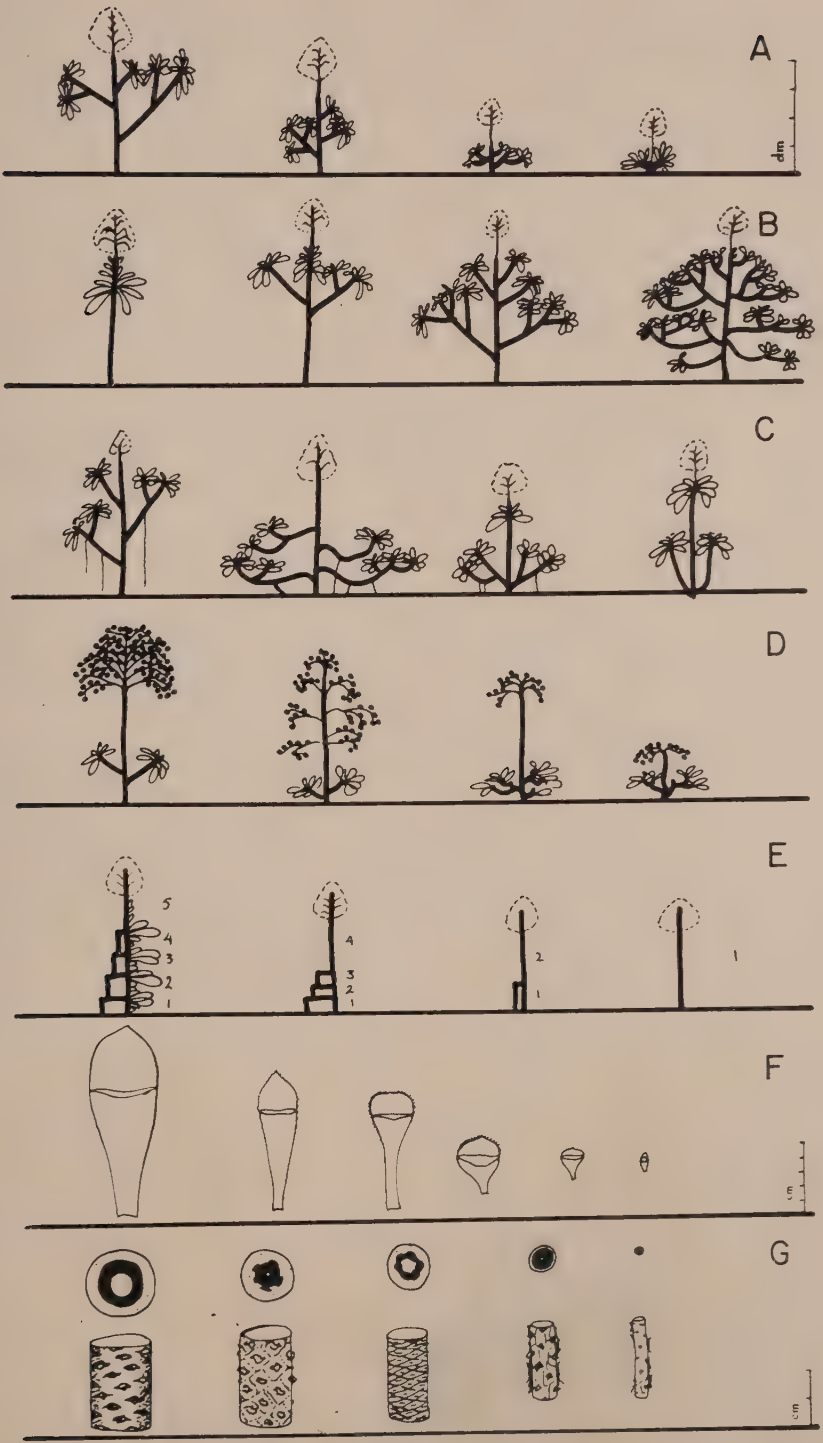

FIG. 8. Criteria of growth form analysis in Aeonium.

A—length of the shoot
B—degree of branching
C—height above ground of the lateral shoots
D—size of the inflorescence
E—duration of the morphogenetic cycle
F—leaf sizes
G—lignification of the axis

pendently in the Holochrysa (*A. undulatum*), the Urbica (*A. ciliatum*), the Canariensia (*A. cuneatum*) and the Goochia (*A. caespitosum*). In view of the great differences between these species we are forced to assume that it is an adaptive specialization rather than a primitive condition.

3. Production of inflorescences.
   a. The size of the inflorescence (Fig. 8 D). The largest inflorescences occur in the sections Megalonium (*A. nobile*), Urbica (*A. percarneum*) and Holochrysa (*A. webbii* and most of the others). Lax inflorescences of considerable volume are found in the Canariensia, while the smallest inflorescences occur among the xeromorphic Urbica and Goochia. However, some of these have long stalks which make the flowers very conspicuous in the field.
   b. The duration of the morphogenetic cycle (Fig. 8 E). There appears to be a correlation between the size of the inflorescence and the time it takes for one to be initiated at the shoot apex. One might explain this on the basis of nutritional phenomena by saying that the more reserves a plant accumulates the larger it can "afford" to make its inflorescence, but there is more to it than that. In my opinion the slowly developing giant inflorescence of *Aeonimum nobile* is a primitive feature which has been retained from times when the climatic and general habitat conditions were more constant and dependable than at present. It also would appear that plants with slow morphogenetic cycles are more dependent upon large numbers of seeds because the long life history implies that a smaller number of individuals reaches the reproductive stage than in the more rapidly developing species. If a species is to survive it must either produce seeds quickly, or it must produce many of them to insure survival of at least one. Both conditions occur in the Sempervivum group.
4. Leaf types (Fig. 8 F). Considerable variation exists in the Sempervivum group with respect to leaf size and thickness. Most of the Holochrysa have flattish leaves of medium size (5-10 cm); the Canariensia have much longer leaves; in both Urbica and Goochia a progressive reduction in leaf size indicates the xeromorphic adaptation of the species, especially those of subalpine cliffs.

On purely theoretical grounds we can fit these evolutionary trends into a pattern which uses the Holochrysa as a point of departure, with tall, hemixylic shoots with sparse branching, and large inflorescences which develop slowly over a number of years. Diverging from this "primitive" growth form I can visualize a trend towards low, herbaceous, large leaved rock plants (the Canariensia), compact, twiggy, dense bushes (the Urbica), and sprawling or hanging cliff plants (the Goochia). Fortunately, I have evidence of quite another kind to give support to this theory: the sizes of areas of the species and species groups.

Geographic distribution

Willis (1922) pointed out that wide geographic ranges, especially disjunct ones, are often due to the great antiquity of a population; small areas are typical of more recently evolved populations. Other explanations are possible: wide-spread groups may be more efficient in their dispersal, they may have greater ecological versatility, or their particular ecological requirement may be fulfilled over extensive areas. On the other hand, narrow ranges may be explained not only by recent origin of the population, but by ineffective dispersal, poor ecological adjustment and other factors resulting from depauperation of the gene pool.

When the wide distribution of the Holochrysa is considered (Table II) there can be no doubt that this is an ancient group of plants. The East African *Aeonium leucoblepharum,* long separated from the other members of the genus, and apparently not a very plastic population, belongs to the succulent shrubby growth form. Very similar types are found in the Cape Verde Islands and in Morocco.

TABLE II. Size of the areas of species of the Sempervivum group shown by the number of islands on which they occur

Group:	Total spp.	Single island endemics	On 2 islands	On 3 or more islands	Madeira	Cape Verde Islands	African mainland	Growth forms:
Holochrysa	9	3	1	1	—	2	2	ancient, uniform
Megalonium	1	1	—	—	—	—	—	ancient relic
Urbica	11	9	2	—	—	—	—	derived, diverse
Canariensia	8	5	1	—	2	—	—	derived, diverse
Goochia	9	5	4	—	—	—	—	derived, diverse
Aichryson	13	6	2	2	3	—	—	derived, successful hygrophytes
Greenovia	4	2	1	1	—	—	—	derived xerophytes

The Urbica and Goochia, although comparable in number of species and better adapted to dry habitats, are strictly endemic to the Canary Islands, many of them to single islands or to one locality. This is in spite of the fact that they have invaded more of the local habitats (see below). Nor is their dispersal mechanism less efficient than that of the Holochrysa; all species of Aeonium have tiny seeds without obvious devices for transportation. Only one explanation remains: the Holochrysa, with the most disjunct distribution, are the oldest group of the genus Aeonium. In the long evolutionary history of the whole genus these plants have stuck most closely to the original architectural plan.

Figure 9 is a graphic representation of the evolutionary status of all species, based upon this point of view.

Ecological significance

Throughout my account of the growth forms I have alluded to the habitats in which the several forms are at home. The habitats of the Canary Islands are differentiated primarily by climatic zonation and by the age and degree of erosion of the substrate (Table III). In each climatic belt there are unmodified igneous rock formations, smaller and larger soil pockets and sometimes deeper, layered soils. We may quickly summarize the ecological distribution of the species of Aeonium in the Canaries by referring to the appropriate climate and soil symbols listed in Table III:

TABLE III. Key to the ecological distribution of Aeonispecies (numbers refer to lists in the text)

Climate	Altitude	Climax	Large Soil Pockets	Small Pockets	Crevices
dry subalpine	above 1,800 m.	Spartocytisus, Adenocarpus	I A	I B	I C
cool	1,500 m.-1,800 m.	Pinus canariensis	II A	II B	II C
cloud belt	300 m.-1,500 m.	Laurus, Ocotea, Persea	III A	III B	III C
humid, low precipit.	0-300 m. (N. exp.)	Kleinia, Euphorbia	IV A	IV B	IV C
dry, warm	0-300 m. (S. exp.)	Launaea, Plocama etc.	V A	V B	V C

Section Holochrysa: Most species in IV A (*A. holochrysum, A. manriqueorum*)

Section Megalonium: the monocarpic *A. nobile* in IV B

Section Urbica:
- *A. percarneum* in IV A
- *A. ciliatum* in IV B, III B
- *A. haworthii* in III B
- *A. castello-Paivae* in V B
- *A. urbicum* in IV B

Section Canariensia:
- *A. cuneatum* in III B, III C
- *A. palmense* in III B
- *A. subplanum* in III C
- *A. canariense* in IV B
- *A. tabulaeforme* in IV C

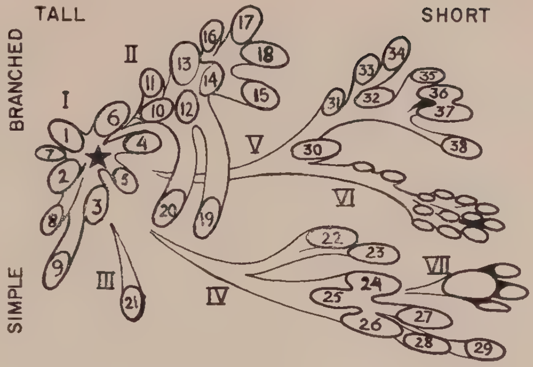

FIG. 9. Evolutionary status of the Sempervivum group, especially with respect to the stature and density of branches. The hypothetical ancestor is indicated by a star. Key: I. Genus Aeonium, section Holochrysa

1. Aeonium manriqueorum Bolle
2. A. holochrysum Webb & Berth.
3. A. gorgoneum J. A. Schmidt
4. A. arboreum (L.) Webb & Berth.
5. A. leucoblepharum Webb ex Rich.
6. A. balsamiferum Webb & Berth.
7. A. rubrolineatum Svent.
8. A. undulatum Webb & Berth.
9. A. webbii Bolle

II. Genus Aeonium, section Urbica

10. A. percarneum (Murray) Pit. & Proust
11. A. gomerense Praeger
12. A. ciliatum (Willd.) Webb & Berth.
13. A. haworthii Webb & Berth.
14. A. valverdense Praeger
15. A. burchardii Praeger
16. A. decorum Webb ex Bolle
17. A. castello-Paivae Bolle
18. A. lancerottense Praeger
19. A. hierrense (Murray) Pit. & Proust
20. A. urbicum (Chr. Sm.) Webb & Berth.

III. Genus Aeonium, section Megalonium

21. A. nobile Praeger

IV. Genus Aeonium, section Canariensia

22. A. cuneatum Webb & Berth.
23. A. glutinosum (Ait.) Webb & Berth.
24. A. canariense (L.) Webb & Berth.
25. A. palmense Webb ex Christ
26. A. subplanum Praeger
27. A. virgineum Webb ex Christ
28. A. glandulosum (Ait.) Webb & Berth.
29. A. tabulaeforme (Haw.) Webb & Berth.

V. Genus Aeonium, section Goochia

30. A. goochiae Webb & Berth.
31. A. viscatum Webb ex Bolle
32. A. lindleyi Webb & Berth.
33. A. saundersii Bolle
34. A. sedifolium (Webb ex Bolle) Pit. & Proust
35. A. smithii (Sims) Webb & Berth.
36. A. cruentum Webb & Berth.
37. A. spathulatum (Hornem.) Praeger
38. A. caespitosum (Chr. Sm.) Webb & Berth.

VI. Genus Aichryson

VII. Genus Greenovia

Section Goochia:

A. goochiae in III B and IV B
A. viscatum and *lindleyi* in IV B
A. saundersii in IV C
A. sedifolium in V C
A. caespitosum in II C
A. cruentum and *spathulatum* in I C

These findings, when summarized, show that the tall, shrubby species of the Holochrysa and Urbica are all restricted to the humid coastal zone (IV A and B) in fairly good soil. Monocarpic species are generally found in smaller soil pockets or crevices. Compact bushes occur in the dry subalpine and coastal rock formations. One may visualize from this account an evolution of ecological requirements within the genus Aeonium.

That the growth forms of these plants have ecological as well as evolutionary significance is further demonstrated by the communities of which they are a part. The primitive Aeoniums of shrubby habit are found in association with other crassicaulous shrubs (Euphorbia, Kleinia and others). The candelabrum forms of the Urbica are accompanied by other similar plants with arching woody stems and leafy rosettes. In the subalpine region, where the Aeoniums are compact, twiggy bushes with long inflorescence stalks, this same habit is affected by Pterocephalus, Lotus, Chrysanthemum, Cheiranthus, Carlina, etc.

Natural selection must be held responsible for this strong convergence. Along the wind-blown crests of the cloud belt only those Aeoniums could survive whose branches are low and firmly anchored by adventitious roots. In their ascent to the subalpine zone the Aeoniums were selected for compactness of vegetative body and strongly seasonal growth pattern. In places where soil was limited to small pockets and crevices, the root systems could not support elaborate, branched plants. But those species which occasionally failed to produce lateral shoots and could flower without forming branches proved well suited to live in such limited spaces. Specific differences developed in due course among such ecologically and geographically isolated populations. There is very little genetic isolation in the Sempervivum group, even in the field. Praeger (1929) reports 32 natural hybrids, of which 25 are between species of Aeonium; 26 of the 38 species are implicated. Yet in the field these hybrids are rare. One possible explanation of this paradox, suggested by Anderson (1948), is that there are no suitable habitats for hybrids having requirements intermediate between the requirements of the parent species.

Confirmation of the ancestral nature of the Holochrysum group can also be gained from the ecological association of these plants: most of the Goochia and Canariensia, and many Urbica are now associated with plants of different geographic affinities; they have established themselves in the *barrancos* of the laurel forest, in the *massifs* among the subalpine scrub of Mediterranean affinity. Only the Holochrysa and some of the succulent Urbica remain associated with the "ancient African" semidesert genera in whose company they must have invaded the islands (Euphorbia groups Diacanthium and Pachycladae, Kleinia, Ceropegia). The Holochrysa appear to be primitive morphologically, ecologically and sociologically.

Conclusion

Adaptive radiation is an aspect of evolution in which botanists are only beginning to take an active interest. I hope there are indications in this paper of the research opportunities in the ecological evolution of the shoot system of the higher plants. Nor is it necessary to limit the investigation to the macroscopic features which I have discussed. I consider the growth form as an end product of morphogenetic processes in which the cells of the shoot apex play a vital part. Anatomical studies of the shoot apex, leaves and stems will all provide data which refine or modify conclusions based upon growth forms.

Praeger's Sempervivum group is especially illustrative because of its great development within the Canary Islands, where many modes of life have been realized by members of the genera Aeonium, Aichryson and Greenovia. But there is no reason why this line of inquiry should be limited to such exotic places, and I hope that an increasing number of ecologists will turn their attention to growth forms of plants on the continents. The study of plant forms occupies a key position in botanical science; it is important to the taxonomist, the morphologist, the ecologist and the plant geographer.

Summary

1. The genus Aeonium (Crassulaceae) is centered in the Canary Islands, where 32 of the 38 species are found. Ancestors must have reached the Canaries in the first part of the Tertiary, if not earlier. The area of the genus includes the East African mountains.

2. The group presents an example of adaptive radiation with respect to the growth forms of the species. Some are shrubby, some are unbranched monocarpic plants, others are sessile rosettes with stolons, dwarf shrubs and hanging rock plants.

These forms can be derived from one another through modifications in the thickness, length and density of the branches, size of leaves and inflorescences (Fig. 7).

3. On the basis of the range of distribution, morphology, and ecological association I suggest that the shrubby species are closer to the ancestral form than any of the smaller species.

4. Each growth form has clear selective advantages in the habitat where it occurs. Habitats are characterized by climatic condition and soil development. The ancestral forms grow along the coast in loamy soil, exposed to the trade wind; derived species are distributed in dry rubble, in crevices in the subalpine zone and in the cloud belt.

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FACTORS IMPORTANT TO YELLOW BIRCH ESTABLISHMENT IN UPPER MICHIGAN

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Increasing the proportion of yellow birch (*Betula alleghaniensis* Britton) in the northern hardwood type should also increase the economic return from management. Under current market prices the stumpage value of yellow birch is about double that of sugar maple (*Acer saccharum* Marsh.), the next most valuable species in the type. The use of yellow birch for veneer accounts for most of its high value. In upper Michigan about 30% of the net volume of this species is sold as veneer compared to only 7% of the volume of sugar maple.

The proportion of yellow birch stems in the old-growth northern hardwood stands is seldom over 12% (Lake States 1935). In this type it is most commonly found as single trees on the edge of small openings or occasionally in small groups where the more tolerant species have died out or been destroyed by a catastrophic type of disturbance. Yellow birch seldom occurs as a pure stand except on relatively small areas that have been opened and mineral soil exposed, such as by windthrow, light burns, or abandoned clearings. However, in the hemlock-yellow birch sub-type (Soc. Amer. Foresters 1954), which occurs on mesophytic sites, yellow birch commonly makes up 25% or more of the stand basal area. In second-growth stands the percentage is usually less, the amount seeming to vary with the soil moisture conditions and species association.

Some regeneration studies have been made in the north central and northeastern portions of the botanical range of yellow birch, but very little work has been reported in the Lake States, which are in the western portion. Although the general silvical requirements of this species are fairly well known, particularly as the tree reaches the larger size classes, little information is available on the early stages of establishment and growth in the Upper Peninsula of Michigan. The reasons for the lack of sufficient yellow birch reproduction after cutting in other regions are generally considered to be the relative intolerance of the species (Baker 1949, Graham 1941), browsing by animals, and more specific seedbed requirements than its competitors.

A study was begun in the Upper Peninsula of Michigan in the fall of 1952 to determine (1) the influence of seedbed conditions on the regeneration of yellow birch, and (2) the relative importance of physical and biotic factors on the establishment and early growth of yellow birch seedlings. In the area selected for study, all seed-bearing trees except yellow birch and a few white pine and hemlock were cut during the winter of 1952-53, and the area was disked in the fall of 1953. This paper summarizes the changes that occurred during four growing seasons after disking and discusses results of special studies on the factors affecting the early growth of yellow birch.

Literature Review

Preliminary work in Upper Michigan on yellow birch regeneration has been aimed principally at the development of saplings in relation to light and competition of associated vegetation. Zillgitt and Eyre (1945) reported that creating small openings up to 0.1 acre in size by means of group selection cuttings resulted in the greatest number per acre and the highest percentage of yellow birch of the six cutting methods examined. The invasion of shrubs in the larger openings was thought to be a significant factor in the reduction of initial stocking, but the surviving yellow birch grew at a considerably faster rate than those in the smaller openings.[2] Similar results in small openings, designated as patch cuttings, were found by Jensen (1950) in New Hampshire. Clear cutting appears to create unfavorable conditions for the relatively slow-growing yellow birch (Cunningham 1953, Zillgitt and Eyre 1945).

The residual stocking that favors the establishment and best development of seedlings has not been determined. The literature indicates a regional variation. In Quebec, Linteau (1948) suggests that a canopy permitting at least 30% full sunlight is best for establishment but that if continued it will retard seedling development. A heavy canopy, letting through less than 10 per cent full sunlight, prevented seedling development, leaving plants in a weakened condition and susceptible to injury by adverse site conditions. He recommends openings of about ½-acre when group selection cuttings are made.

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[1] Maintained at St. Paul 1, Minn., in cooperation with the University of Minnesota.

[2] Unpublished data, Lake States Forest Experiment Station.

Jarvis (1957) found in a study in Ontario that rapid height growth was made under approximately 70% full sunlight. This growth was maintained the second growing season even though the weather was abnormally hot and dry. To provide the best light conditions at ground level, Jarvis (1956) suggested reducing the main canopy to about 40% closure. Cunningham (1953), summarizing the work in the Great Lakes-St. Lawrence forest region, suggested that 60 to 80% of the stand should be removed.

All investigators emphasize the necessity of providing a scarified seedbed. In the regions studied, very few yellow birch became established or developed well on undisturbed hardwood litter (Burton 1956, Burton and Leslie 1953, Cunningham 1953, Jarvis 1957, Koroleff 1954, Linteau 1948, Sowers *et al.* 1956, Webb, King, and Patric 1956, Zillgitt and Eyre 1945). Mineral soil exposed by summer or fall logging was considered the best seedbed in Upper Michigan (Eyre and Zillgitt 1953) and in the Alleghenies (Sowers *et al.* 1956) and Adirondacks (Webb *et al.* 1956). In Ontario, Jarvis (1957) found that a mixture of humus and mineral soil was the most favorable. Compacted mineral soil did not favor early growth, but it did not restrict germination. Cunningham (1953) considered humus the best seedbed in the Great Lakes-St. Lawrence region.

Several factors other than an unfavorable seedbed of hardwood leaf litter are responsible for mortality in young reproduction. In Quebec, Linteau (1948) found late frost the main cause of seedling mortality. During the two growing seasons of his observations, frost caused 51% of all losses. Only seedlings with vigorous shoot and root development survived. Some losses were attributed to high temperatures and lack of soil moisture, but this cause was not considered too important. The development of yellow birch seedlings during the first growing season was considered the critical factor that determined survival. This conclusion is supported by a study in Ontario (Jarvis 1957) where yellow birch had excellent height growth on hot, dry, exposed sites when the roots were well established. Yellow birch was noted as being sensitive to extreme temperatures (Jarvis 1956), although the mortality attributed to this factor was not great.

A review of the literature on animal damage indicates that most damage is caused by the snowshoe hare (*Lepus americanus phaenotus* J. A. Allen) and the white-tailed deer (*Odocoileus virginianus borealis* Mill.). Dahlberg and Guettinger (1956) rated yellow birch second-choice deer browse in Wisconsin, Pearce (1937) placed it at the top of the preferred list in the Adirondacks, and Gill (1957) gave the species a medium but quite variable palatability rating in Maine. In northeastern Wisconsin, which has maintained a high deer population, damage to both paper birch (*Betula papyrifera* Marsh.) and yellow birch has been extensive. In the same area Swift (1949) found 20% of the birch[3] reproduction was browsed by white-tailed deer, and Stoeckeler *et al.* (1957) reported most deer damage to young yellow birch was in thinly stocked or old-growth sawlog stands. Exclosure studies in a thinly stocked stand showed that about five times more yellow birch within the fenced area reached 4.5 ft than on the unfenced area. After 4 years of protection, the reproduction in the sawlog stand ranged from 3 to 6 ft in height, and on the unfenced area the average height was less than half a foot.

In Upper Michigan, Graham (1954, 1958) found that deer browsing was responsible for vegetation changes in the northern hardwood-hemlock type. By 1947 overbrowsing was eliminating the reproduction of white-cedar (*Thuja occidentalis* L.), hemlock (*Tsuga canadensis* (L.) Carr.), and yellow birch, and stunting the growth of hard maple reproduction. Exclosures established in 1949 were re-examined in 1957 and showed the reproduction was less abundant on the unfenced study areas. Graham concluded that deer have influenced the composition of the forest to the extent that the future forest may have less than 5% yellow birch although originally the species probably formed about 30%.

Webb *et al.* (1956) found little effect of deer browsing in mature hardwoods of northern New York, apparently because the chances of survival of these species under dense shade are not good. However, yellow birch may become established when the deer trample seed into the ground or expose mineral soil with their hoofs. Curtis and Rushmore (1958), in studies in the same locality, concluded that deer browsing was a less limiting factor than competition, although both factors tended to retard seedling development. In Ontario, Jarvis (1957) found that deer browsed 34% of the 3,000 quadrats established in 1955 and he concluded that, even if the seedlings are not killed by browsing, they will probably become misshapen and will not develop into good quality trees.

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[3] A check of the original data shows that this was yellow birch reproduction.

Red squirrels (*Tamiasciurus hudsonicus hudsonicus* (Erxleben) in Quebec were reported by Linteau (1948) to cause injury to 14% of the seedlings on the plots under a full canopy. In later correspondence[4] Linteau stated, "Apart from feeding on the seed, red squirrels cut a number of seedlings before their stems suberized, that is, during the first month after germination. The seedlings were left on the ground without further action."

Insects and disease generally cause little damage to yellow birch seedlings. Linteau (1948) found that the spring cankerworm (*Paleacrita vernata* (Peck)) killed 9% of the seedlings at the full-canopy station and none at the open and partial-canopy stations.

Thus the literature indicates that the influence of factors affecting the regeneration of yellow birch varies among regions. Although most investigators are in agreement on the type of seedbed that is desirable, they tend to disagree on the conditions favoring seedling development and those causing mortality. In the northeastern portion of the range the best seedling development occurs under a canopy permitting at least 30% full sunlight, while in Ontario about 70% full sunlight is required for best development. Frost is the principal cause of mortality in the northeastern portion of the botanical range, but is not considered serious in other regions. High soil temperature, lack of soil moisture, and browsing by animals are often considered to be more important for the south and west.

This study evaluates these factors in the Upper Peninsula of Michigan.

DESCRIPTION OF THE STUDY AREA

The area selected for study was a 20-acre tract of hemlock-yellow birch type averaging 14.6 M board feet (Scribner) per acre. Yellow birch comprised 25% of the total volume. The predominant species was eastern hemlock which made up 50% of the original stand. The remaining stand volume was 18% red maple (*Acer rubrum* L.), 4% sugar maple, 2% white-cedar, and 1% white pine (*Pinus strobus* L.) and balsam fir (*Abies balsamea* (L.) Mill.). Defect in the stand averaged 40%, leaving a merchantable volume of 8.7 M board-feet per acre.

The study area lies on an east-west till plain with level to gently rolling topography. The elevation is approximately 1100 feet, or 500 feet above the level of Lake Superior. The soil is an imperfectly drained fine sandy loam averaging more than 60 in. in depth with a strongly cemented hardpan at 16 in. In the spring after the snow melts, the water table is often within 6 to 8 in. of the surface and remains at a high level for an extended period.

Precipitation averages 34 in. a year and is well distributed, with only very short intervals between measurable amounts. Winter snow depths of 4 ft are common. The mean temperature for the growing season, June 1 to September 30, is 60° F.

FIELD PROCEDURE

During the fall of 1952 and the following winter, all trees of seed-bearing size except yellow birch and a few white pine and hemlock were cut on the 20-acre tract. This left a well distributed yellow birch seed source on the area, but it also left a relatively undisturbed seedbed.

During the following September, prior to seed fall, one-half of the area was disked with an Athens disk. This treatment was restricted to the open areas and the slash-free areas along skid trails (Fig. 1).

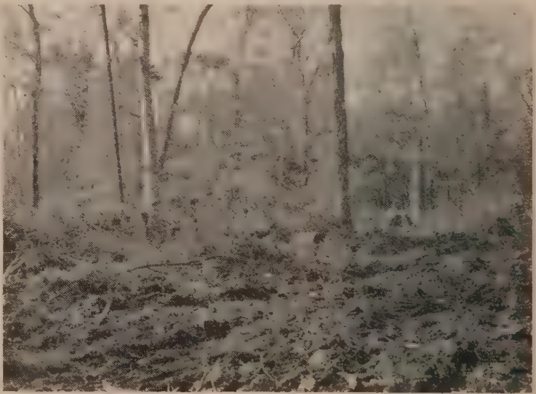

FIG. 1. Study area with disked portion in the foreground.

Immediately after disking, 400 one-quarter mil-acre permanent sample plots were established to determine the amount of reproduction and changes in it. The plots were stratified by percentage of area disked; the classes were 0, 25, 50, 75, and 100%. The number of yellow birch seedlings was tallied by 5 height classes; the presence of other species was noted, but not the number or size of reproduction.

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[4] Personal communication of Feb. 25, 1957, from Dr. André Linteau, Dept. of Northern Affairs and National Resources, Faculty of Forestry, Laval University, Quebec.

Special studies on the effect of mammals, the influence of shade and soil temperature, and the changes in ground water level were established in the area as the seedlings developed.

TREATMENT EFFECT ON YELLOW BIRCH REPRODUCTION

The cutting favoring yellow birch seed trees in itself contributed greatly to the abundance of yellow birch reproduction. On the undisked area in September 1953, one growing season after cutting, yellow birch was present on 72% of the quadrats and averaged slightly over 32,000 per acre. Some of the reproduction was advanced growth as evidenced by the fact that 15% of the area had seedlings more than 6 in. in height. The total number per acre (Table I) and the growth into taller height classes (Figs. 2 and 3), however, have been much less than on disked quadrats.

Disking one full growing season after cutting resulted in a slight loss in the per cent of the area stocked but left a relatively uniform though much smaller number of seedlings per acre. The loss was largely the result of direct physical action on the seedlings.

TABLE I. Yellow birch: Per cent of quadrats stocked and thousands of seedlings per acre at end of growing season, by percent of area disked

Percent disked	QUADRATS STOCKED (percent)					NUMBER OF SEEDLINGS PER ACRE (thousands)				
	1953	1954	1955	1956	1957	1953	1954	1955	1956	1957
0	72	79	56	45	66	32	34	29	14	13
25	47	94	65	53	47	13	159	64	12	6
50	52	100	86	62	67	10	214	141	74	71
75	77	100	100	77	62	11	378	278	152	91
100	42	96	92	67	71	11	243	248	121	81

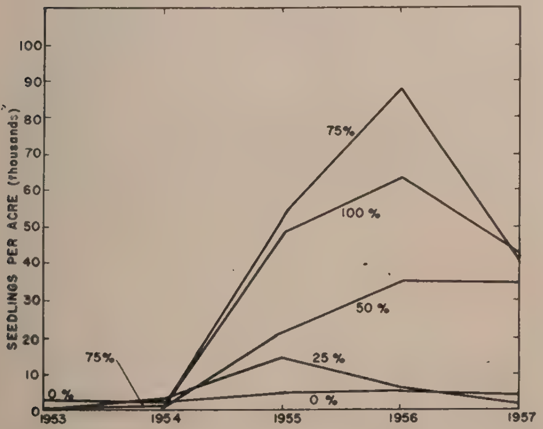

FIG. 2. Number of yellow birch seedlings per acre in the 6- to 12-inch height class by per cent of area disked, 1953 to 1957.

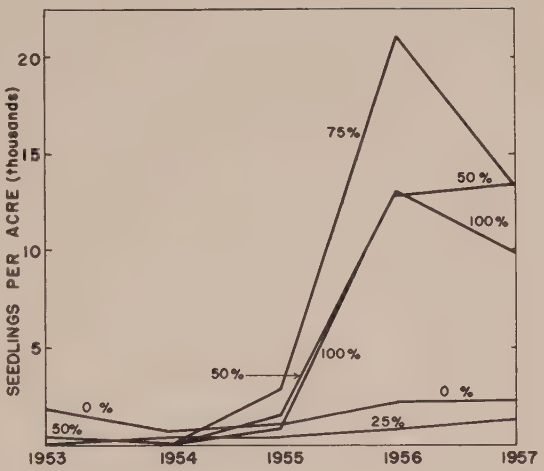

FIG. 3. Number of yellow birch seedlings per acre in the 12- to 72-inch height class by per cent of area disked, 1953 to 1957.

In September, 1954, one growing season after disking, 94% or more of the scarified quadrats were stocked, and the number of seedlings per acre had increased with the area disked. The number of seedlings ranged from 159,000 per acre on the lightly disked areas to 378,000 per acre on quadrats with 75% coverage. After four growing seasons, the quadrats with 50% or more of their area scarified still have by far the greatest number of yellow birch seedlings per acre and the largest percentage of stocked quadrats.

Each year fewer new seedlings became established as the seedbed conditions grew less favorable. The effect of scarification had essentially disappeared by the third growing season.

Height growth has been most rapid on quadrats with 50% or more of their area scarified. Growth into the 6- to 12-in. height class was rapid during the second year after disking and into the next taller class (12- to 72-in.) the third year. During the fourth growing season, the 12- to 72-in. height group showed an increase in per cent of total seedlings although the number was less.

Seedling survival has been relatively low over the four growing seasons. The highest survival, 38%, has been on the unscarified area and the lowest, 4%, on quadrats with only 25% of their area disturbed. Most of the mortality occurred during the 2 years after treatment, the lighter disking having the highest mortality rate of all classes during the first year.

Other Factors Affecting Seedling Establishment and Growth

Following seedbed scarification supplemental studies were established on the area to evaluate some of the factors affecting germination and early growth. The factors considered in this section are seed production, seedbed conditions, competition and the survival of competing species, precipitation and temperature, shade requirements, frost, and injury by animals. Of these, this study shows that the most important factors affecting germination and early growth are, respectively, seedbed condition and amount of overhead shade.

Seed Production

The seed production of yellow birch, on a rating scale of bumper, good, medium, poor, and failure, was good in 1952 and 1953. Disking was completed prior to the dispersal of the 1953 crop. In 1954 the seed production was rated medium, in 1955 poor, and in 1956 medium.

Data on the amount of seed produced by the residual trees were not collected. That an adequate amount was produced to regenerate the area completely is indicated by the number of seedlings that became established. In one portion of the tract averaging only 4 seed trees per acre, the number of seedlings on quadrats that were 75% disked averaged 535,000 per acre. This figure, considered in conjunction with the germinative capacity of yellow birch, which averages 27% (U. S. Forest Service 1948), indicates the vast number of seed produced by yellow birch trees (Lake States Forest Expt. Sta. 1936).

Seedbed Conditions

The occurrence of yellow birch seedlings was related to the surface soil moisture as well as to the physical condition of the seedbed. The seed of yellow birch is the smallest and lightest of any competing trees in the type, averaging 447,000 per pound (U. S. Forest Service 1948). In order to germinate seeds must lie in a moist place, and to become established they must be on a medium favorable to rooting. Because seedlings are quite small and usually of low vigor, they do not make rapid shoot or root growth in this early period. They cannot survive much if any competition, particularly where moisture is limited.

On the other hand, if moisture is plentiful during this critical period, seedlings will become established, even with heavy competition. They were observed in areas of dense sod and horsetails when water was standing in the low areas (Fig. 4). Growth, however, was retarded and survival was low.

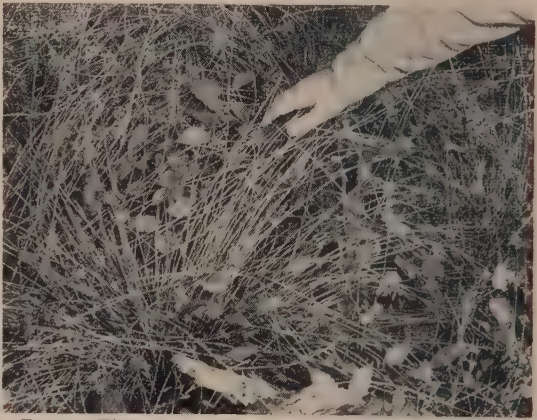

Fig. 4. Three-year-old yellow birch in dense patches of horsetails where water is abundant throughout the growing season.

Patches of undecomposed organic matter, with little mineral soil in the mixture, made a poor seedbed. Probably because of the rapid drying out of the surface layers very few seedlings of any species became established on these areas. Few seedlings were found on matted leaf layers.

The best seedbed for germination and growth of yellow birch was mineral soil mixed with partially decomposed organic matter (Fig. 5). This type of seedbed is capable of high moisture retention and has a relatively smooth but "textured" surface favorable for germination and for rapid establishment of the seedling roots. The microtopography of the area was also important. Most of the seed tended to collect in minute depressions, being either windblown or carried by water. Very few seedlings became established on the ridges un-

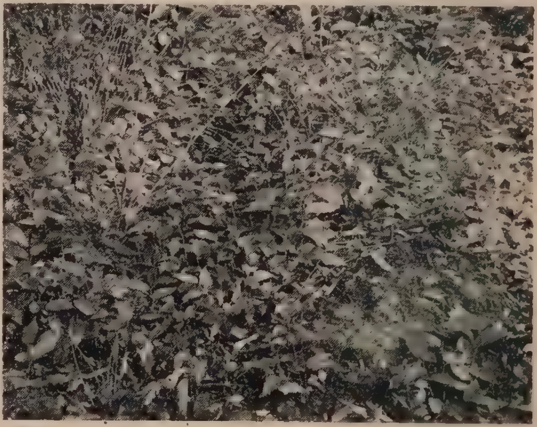

Fig. 5. Two-year-old yellow birch on desirable seedbed of mixed mineral soil and organic matter.

less the seed had lodged against some obstruction (Fig. 6).

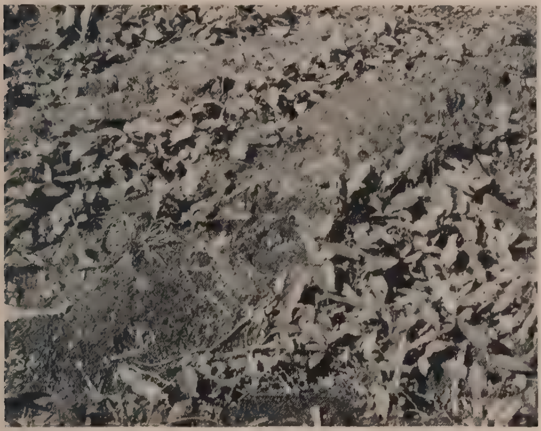

FIG. 6. Influence of micro-topography on yellow birch seedling establishment. Seedlings are 2 years old.

Competition

Under the heavy cutting, the ground vegetation increased very rapidly and completely invaded most of the scarified areas within 3 years. Unless the seeds germinate on a seedbed favorable to early establishment and growth, grass, raspberry, and blackberry bushes overtake and smother the yellow birch. The delay in disking for one growing season, as was done in this study, permitted a year's buildup of the shrubs prior to seedling establishment. On the quadrats with only one-fourth of the area scarified, 60% of the seedlings died the second year, largely as a result of competition from established shrubs. On quadrats that were completely scarified the total number of yellow birch showed a slight increase the same year. The third season, however, 52% of the seedlings were lost on 100% disked quadrats.

The time of year of the seedling mortality has changed with the age of the seedlings, suggesting that competition from shrubs and reproduction becomes more severe as the seedlings grow older. Nearly three-fourths of the loss of the second-year seedlings were over-winter losses. During the third year, mortality was about the same for both seasons; but the trend indicates that growing season losses will become higher in older seedlings.

The competition from residual saplings and poles was not a significant factor affecting seedling development in the early stages of regeneration. The stocking or number of seedlings per acre was not correlated with a competition index based on the distance to the nearest tree and its total height. This factor is expected to become more important as the reproduction develops. Sprouts from red maple stumps, occurring in great numbers and having dense, wide-spreading foliage, make rapid height growth and are the principal competitors with yellow birch. Seedlings of red maple are not as vigorous competitors.

Survival of Competing Species.—Red maple was present on most of the area prior to disking and has continued to be about as well stocked as yellow birch after disking. The greatest loss of red maple during the 4 years occurred on the areas with 75% of the area disked, although it was still present on almost half of the quadrats. A large number of the red maple stems on these quadrats are of seedling origin, which is probably an important factor in the reduction in stocking of the competitive species.

Sugar maple was the next most frequent species; it occurred on 5% of the area that was 50% disked and on 26% of the undisked areas, with percentages for other classifications ranging between these figures. At the end of the fourth growing season, all sugar maple had died on the area with 50% disking, and the undisked areas had only 20% stocking.

Hemlock and balsam fir were present on the area before disking, averaging 29 and 21% frequency, respectively, but these figures decreased to 12 and 8% during the period of observation. Cherry (*Prunus* spp.), aspen (*Populus tremuloides* Michx.), mountain ash (*Sorbus americana* Marsh.), and white spruce (*Picea glauca* (Moench) Voss) occurring on less than 10% of the quadrats, showed a general increase in stocking on the undisked area the first season, but have since shown a general decline. Cedar regeneration has been relatively stable and occurs on about 7% of the quadrats.

Precipitation and Temperatures

The climatic variations observed during the period of study did not appear to exert a direct effect on yellow birch germination and establishment.

Precipitation was well distributed throughout all growing seasons with only 3 periods of over 10 days occurring without a measurable amount. None of these exceeded 13 days' duration. The largest deviation from normal precipitation occurred in 1955 at the beginning of the second growing season after treatment (Table II). Although there were no extended dry periods, the total accumulation was not sufficient to saturate the soil below rooting depth and the ground water table dropped earlier than usual after snowmelt (Fig. 7). The highest annual percentage loss in

TABLE II. April to September distribution of precipitation at Chatham 10 miles east of the Upper Peninsula Experimental Forest, 1953 to 1957[1]
(In inches)

Year	Month						Annual
	Apr.	May	June	July	Aug.	Sept.	
1953	3.97	3.39	4.97	3.73	1.91	4.11	36.05
1954	4.40	3.59	3.23	1.32	1.78	6.44	32.23
1955	2.30	1.43	1.34	2.12	3.12	1.26	27.19
1956	2.30	3.22	3.41	3.97	2.19	2.57	25.17
1957	1.91	3.09	1.72	2.05	2.57	7.17	30.25
Normal	2.26	2.98	3.62	3.16	3.24	4.19	33.49

[1] U. S. Weather Bureau (1953-1957).

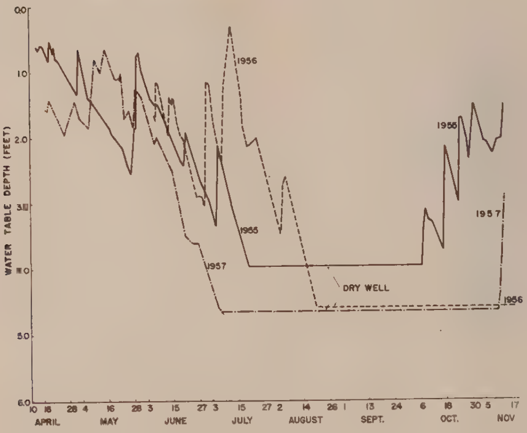

FIG. 7. Fluctuations of the water table under a heavily cut hemlock-yellow birch stand during the third, fourth, and fifth growing seasons after logging.

number of stems was in the 2-year-old seedling stage. However, the mortality was primarily overwinter rather than growing season losses, suggesting that the deficiency in soil moisture during this period may have contributed to a general decline in vigor.

Air temperatures during the period of study were near normal (Table III). Few temperature extremes were experienced; the highest temperature was 99° F on July 26, 1955. Temperatures above 90° F are infrequent in the area, seldom occurring more than 5 days during a growing season. The number of days between fall and spring minimum temperatures of 32° F or lower varied from 99 days in 1956 to 111 in 1957 (U. S. Weather Bur. 1953-1957).

TABLE III. April to September average monthly air temperatures at Chatham 10 miles east of the Upper Peninsula Experimental Forest, 1953-1957[1]
(Degrees Fahrenheit)

Year	Month						Annual
	Apr.	May	June	July	Aug.	Sept.	
1953	37.2	51.2	61.6	66.4	67.2	57.3	43.9
1954	38.9	51.2	63.3	63.9	63.2	53.9	41.7
1955	45.2	53.9	60.9	71.1	69.6	57.7	43.2
1956	36.4	48.2	62.2	60.7	63.0	52.3	41.2
1957	40.5	50.4	59.9	66.5	63.2	54.6	41.2
Normal	38.2	50.0	60.3	66.0	64.4	56.5	41.4

[1] U. S. Weather Bureau (1953-1957).

Soil temperatures at depths of 3, 6, and 12 in. were checked by current-reading mercurial thermometers in 1955 to determine differences under 25, 50, and 75% lath shade cover. The maximum temperatures observed at the 3 in. depth were 72° F under 25% shade and 68° F under the 75% shade. At the 6 and 12 in. depth the temperature averaged respectively about 5° and 10° less. At the 12 in. depth the temperature averaged about 7° higher than in an adjacent virgin stand. Unpublished data from the Upper Peninsula Experimental Forest show that soil temperatures at the 1 in. depth are seldom over 5° higher than at the 3 in. depth. Because of the rapid growth of ground vegetation, high surface temperatures would not be expected after the first few years even in heavily cut stands.

Frost

In the spring of 1955, frost damage occurred on the 2-year-old seedlings that ranged in height from ¼ to about 10 in. That year the earlier part of May had been unusually warm with a maximum daily temperature of 82° F, resulting in early leafing out of all species. Light frosts occurred on May 6, 17, and 18, and a severe frost with a low temperature of 18° F occurred on May 9.

Of the 400 tagged seedlings observed after the leaves were well expanded, 83% were injured by frost. Thirty-six per cent had dead tips varying in length from 1 to 4 in. The taller seedlings had the most severe injury, but the shorter seedlings exhibited some degree of leaf damage. Mortality attributable to frost, however, was very light. At the end of the growing season less than 4% of the frost-injured trees had died, while nearly 5% of those uninjured were lost. The frost damage generally had little effect on the seasonal height growth of yellow birch seedlings (Table IV).

Frost injury was noted again in the spring of 1957. However, only one severe frost on May 16 and one light frost on May 20 occurred after the seedlings had begun to leaf out. Thirty-one per cent of the seedlings were affected, with 25% having dead tips. As in the 1955 injury, height growth was essentially unaffected. The annual growth on these older seedlings, however, was much less than on 2-year-old seedlings.

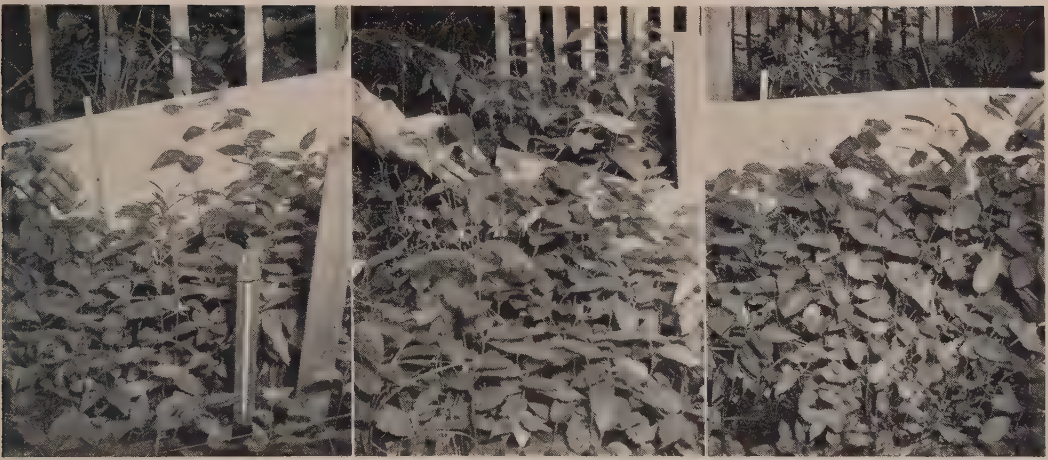

FIG. 8. Development of 2-year-old yellow birch seedlings on scarified seedbeds under three degrees of shade: 25 per cent (left photo), 50 per cent (center photo), and 75 per cent shade (right photo).

TABLE IV. Two-year-old yellow birch: Damage to seedlings by severe frost on May 9, 1955, by injury class

Extent of frost injury	Number of seedlings	Initial Av. height	Seasonal Growth	
			1955	1956
	Percent	*Inches*	*Inches*	*Inches*
Uninjured	17	1.26	5.69	5.76
Leaves frosted	47	2.52	6.34	6.70
Tip killed	36	3.92	5.62	6.89

Frost, although not affecting survival or amount of seasonal height growth to an appreciable extent, appears to be an important factor in the cumulative height development of the seedlings in heavily cut stands. A few weeks after the dead twigs break off, the injury could be mistaken for browsing damage unless carefully examined.

Shade Requirements

One-year-old seedlings generally showed a chlorotic appearance and relatively slow growth over most of the area, the extent appearing to vary with the amount of overhead shade. At the beginning of the second growing season three replications of a shade study, using lath oriented in a north-south direction, were established on the area. Spacing of the lath was designed to give 25, 50, and 75% shade over 4x4 ft plots. Seedlings under each shade cover were tallied by one in. height classes in the spring and again in the fall for two growing seasons.

At the initial measurement of the shade study, 95% of the 3,040 2-year-old seedlings were 3 in. or less in height, with a 0.27-in. difference in the plot average height under each degree of shade. Only 0.35% of the seedlings under the 25% shade and 1.26% under the 50% shade were 4 in. or more tall. At the end of the two growing seasons, 8% of the seedlings under 25% shade and 10% under the 50% shade were taller than 20 in. Only one seedling reached a height greater than 20 in. under the 75% shade. The tallest 3-year-old seedlings were 28, 42, and 24 in. under the 25, 50, and 75% shade respectively. The average height growth under each of the three degrees of shade is shown in Table V. These results indicate the need for increasing the amount of light as the seedlings become older to encourage maximum development.

TABLE V. Influence of shade intensity on height growth of yellow birch seedlings
(In inches)

Percent of shade	Initial height	Av. Ht. Increment		Maximum Ht. Increment	
		1st growing season	2nd growing season	1st growing season	2nd growing season
25	1.53	4.41	5.61	19	8
50	1.80	6.20	4.87	19	22
75	1.55	5.00	2.28	17	6

Seedlings under 50% shade had the best stem and root development and had good leaf color. Under the 75% shade the stems were more succulent and shorter than under the 25 and 50% shade, the root development was poor, and the leaves were unusually dark green and abnormally large. Those under the 25% shade were about the same as unshaded seedlings and had a general chlorotic appearance (Fig. 8).

Injury by Animals

In the fall of 1953 a special study was started to determine, if possible, the effect of small mammals and white-tailed deer on the early establishment of yellow birch seedlings. Eight hardware-cloth exclosures (½ in. mesh, 3 ft square and 2 ft high) and a similar number of control plots (3x3 ft) were established on the 20 acre study area. Four of them were built so that the hardware cloth extended into the ground several in. (Fig. 9). On the rest, the wire extended to within 3 in. of the ground and permitted small mammals to enter if they so desired (Fig. 10). Gross seedling counts were made each spring and fall within each exclosure and on each control plot. Also, 25 seedlings on each plot were permanently numbered and studied to determine mortality, height growth, and damage by mammals or other causes.

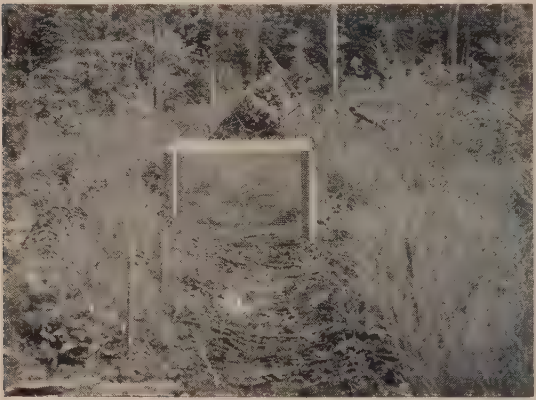

Fig. 9 . Exclosure with unfenced plot in foreground (undisked areas). The hardware cloth extends several inches into the ground.

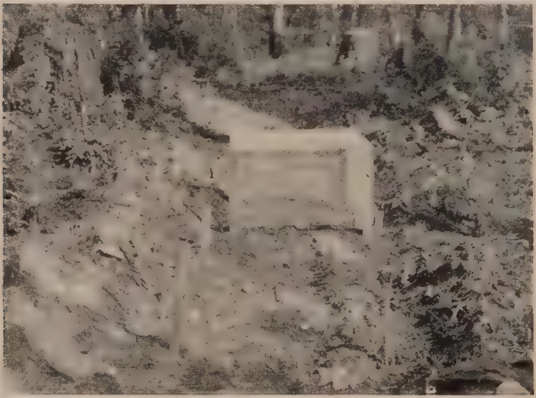

Fig. 10. Exclosure with opening at ground level (disked area).

Small mammals were trapped on three nights each spring and fall using the North American Census of Small Mammals system of trapping. Mammals trapped or observed on the study area include: White-footed mice (*Peromyscus maniculatus gracilis* (Le Conte)), red-backed voles (*Clethrionomys gapperi gapperi* (Vigors)), masked shrews (*Sorex cinereus cinereus* (Kerr), short-tailed shrews (*Blarina brevicauda kirtlandi* (Bole and Mouthrop)), least chipmunks (*Eutamias minimus neglectus* (J. A. Allen)), red squirrels, snowshoe hares, and white-tailed deer. The mouse population on the study area was at a low level between 1953 and 1957. The highest catch per trap night occurred in the fall of 1953 when an average of 17.5% of the traps caught mice; the lowest, less than 1%, was in the fall of 1956. Only a small number of chipmunks and shrews were taken in the traps. A population study made in the spring of 1959 indicates the deer population is approximately 15 per sq. mi., although most of the region outside the experimental forest has a population of 25 deer per sq. mi. However, the population on the study area appears to be gradually rising, judging by the amount of browsing noted recently. Field observations on the snowshoe hare have shown that the 20 acre study area has supported a maximum of 3 animals.

Damage and mortality of yellow birch by deer browsing has been much less than from frost and competition. The amount of browsing did not exceed 19% of the unfenced seedlings at any study period. A slightly higher percentage of the seedlings was browsed in the spring compared to the fall (Table VI). However, there was a greater mortality after fall browsing. The greatest mortality of browsed reproduction was 11%, and this was on 3-year-old seedlings.

Table VI. Total amount of deer browse and associated mortality on yellow birch seedlings by season of year

Date of observation	Live Seedlings	Seedlings Deer Browsed			
		Total		Dead seedlings	
	Number	Number	Percent	Number	Percent
Spring 1955	200	36	18	—	—
Fall 1955	188	30	16	4	2.1
Spring 1956	163	31	19	5	3.1
Fall 1956	135	20	15	5	3.7
Spring 1957	90	8	9	10	11.1
Fall 1957	80	7	9	1	1.2

Snowshoe hare damage on open-grown seedlings was negligible. On the sample areas studied for deer damage, hares browsed on only 3% of the seedlings. However, the amount of nipping was greater on the lath-shade study plots, and the amount increased as the degree of shade increased. In 1956 the hare-nipped seedlings amounted to 9, 10, and 16% under 25, 50, and 75% shade, respectively. Some possible reasons for this may have been differences in succulence of the seedlings or in their abundance.

There was no evidence of damage to small seedlings by mice, chipmunks, shrews, or red squirrels.

CONCLUSIONS

Results of this preliminary study indicate that scarification exposing mineral soil on 50% or more of the seedbed will increase the proportion of yellow birch in northern hardwood stands. The data suggest that a method of partial cutting, in conjunction with snow-free logging or mechanical scarification, would favor the environmental conditions required by this species. Removal of the overstory canopy to let through approximately 50% of full sunlight appears to be the most favorable for establishing the seedlings and for providing enough shade to retard brush and weed competition and reduce the influence of frost.

Recommended silviculture in the type now includes planned salvage cuts 3 to 5 years after the initial cutting. These cuts would gradually increase the amount of light for maintaining growth on established reproduction. Release cuttings may be necessary to free the most promising trees from overhead competition and to provide growing space for rapid stem development of this valuable species.

SUMMARY

Although adequate seed crops occur frequently, the proportion of yellow birch seedlings is generally lower in second-growth stands than before cutting. Because it is the most valuable species in the type, largely because of the yield of veneer, the economic return from management should be higher if the proportion of yellow birch could be increased. The literature indicates a regional variation in the factors affecting its establishment and early growth. A study was begun in the Upper Peninsula of Michigan, near the western limits of the natural range, to determine the effect of seedbed condition and the relative importance of home environmental conditions on yellow birch in this area.

The most important factor affecting the establishment and early growth was the seedbed condition, as adequate seed was nearly always present. Undecomposed organic matter and undisturbed hardwood leaf litter resulted in the least number of yellow birch seedlings and the poorest growth of those that did become established. Mineral soil mixed with partially decomposed organic matter was the best seedbed, if a desirable texture and topographic condition existed. It resulted in suitable moisture conditions for germination and was the most favorable for rooting and seedling development.

Scarification was necessary to obtain these desirable conditions. Exposing mineral soil on 50% of the seedbed yielded the best stocking, number per acre, and growth of yellow birch seedlings. The quadrats with 75% of their area disked still had 91,000 yellow birch seedlings per acre or 24% survival at the end of four growing seasons. Undisked areas averaged 38% survival and had 13,000 seedlings per acre. Height growth, however, was poor; and competition from associated species, especially red maple sprouts, was beginning to dominate the yellow birch.

The period of greatest seedling loss varied with age of the seedlings. Nearly three-fourths of the 2-year-old seedlings died between leaf fall in the autumn and full leaf in the spring. Three-year-old seedling loss was about the same during the winter as the summer.

Surface soil moisture appeared to be a critical factor during the germination and early establishment period. Where moisture was adequate throughout the growing season, yellow birch seedlings became established in sodded areas and in patches of horsetail. Growth in these conditions, however, was retarded and seedling development was poor.

Competition from shrubs under the heavy cutting caused much mortality and rapid disappearance of favorable seedbeed conditions. Blackberry and raspberry bushes completely invaded the area within 3 years and suppressed and smothered many yellow birch seedlings. The rate of invasion was partially correlated with the amount of scarification. Competition from tree species was of less importance. Sprouts of red maple were the most competitive because of their rapid height growth and widespreading crowns. Seedlings of red maple and other species were not strong competitors.

Species composition of the reproduction is changing slowly. Yellow birch and red maple, particularly the sprouts, are tending to become dominant, with yellow birch the most abundant on the scarified areas. Other species are showing a general decline and, after four growing seasons, constitute less than 20% stocking. In order of importance the species are red maple, yellow birch, sugar maple, hemlock, and balsam fir. Other species of minor importance are cherry, northern white-cedar, mountain ash, aspen, and white spruce.

Soil temperatures are increased by heavy cuttings; however, temperatures above 72°F at a depth of 3 in. are apparently unusual. Surface temperatures, though higher, are not thought to be

critical as vegetation rapidly covers the ground and restricts direct insolation.

Yellow birch seedlings were frequently injured by spring frosts. However, mortality from this cause was negligible. Seasonal height growth was relatively unaffected although repeated frosts caused reduction in total height. Severity of injury was associated with seedling height during early establishment and may be correlated with seedling vigor or hardiness. After the frost-killed tips have broken off, the injury appears similar to deer browsing.

Development of established seedlings was influenced by the amount of sunlight. Fifty per cent shade resulted in the best stem, leaf, and root development and the greatest amount of seasonal height growth. Twenty-five % shade was better than 75% shade.

Seedling height growth in unshaded areas was greatest on quadrats having 75% of their area disked. Although mortality was high, the growth into the larger size groups was more rapid than on quadrats having a smaller amount of disking.

Since the populations of deer and snowshoe hares were at a relatively low level between 1953 and 1957, the damage and mortality were light on the unfenced study areas. No mortality was attributed to hare nipping, but the amount of nipping increased with an increase in shade; 16% of the seedlings were nipped at the 75% lath-shade plots. The white-footed mouse, red-backed vole, masked shrew, short-tailed shrew, least chipmunk, and red squirrel did not damage any of the seedlings.

The silvicultural requirements that appear most favorable for increasing the proportion of yellow birch in northern hardwood stands are: (1) scarification to expose mineral soil on 50% or more of the area; (2) reduction of the overstory canopy to let through approximately 50% of full sunlight; and (3) planning a salvage cutting 3 to 5 years after the initial cut to gradually increase the amount of light for maintaining growth of the established reproduction.

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THE COMPOSITION OF THE LAKE MCDONALD FOREST, GLACIER NATIONAL PARK

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The area surveyed in this study is in the southwest part of Glacier National Park and lies only 5-7 mi. west of the Continental Divide. McDonald Valley is one of the larger and better known valleys on the west slope of the Park. Lake McDonald, the largest body of water in the Park, is approximately 10 mi. long and between 1.5 and 2 mi. wide. It owes its existence to a Pleistocene valley glacier which deposited sediments at the lower end of the valley to form a moraine which dammed up the basis and produced the lake. The glacier is calculated to have been at least 1400 ft thick, for the lake attains a depth in some places of 400 ft and there are evidences of moving ice on the ridges paralleling the lake 1000 ft or more above the present water level.

The term, Lake McDonald Forest, is the author's own coinage and refers to that part of McDonald Valley near the lake and below 4200 ft elevation (Fig. 1). It is felt that this constitutes a rather natural area since the slopes above 4200 ft or 4300 ft typically become more precipitous and the aspect of the forest exhibits gradual but marked changes. To the south and west of Lake McDonald lies the extensive Flathead Valley with an average elevation of approximately 3000 ft. West Glacier has an elevation of 3190 ft which is almost precisely the same as that of Lake McDonald. Approximately six mi. east is the Continental Divide with an average elevation in the region of about 8000 ft.

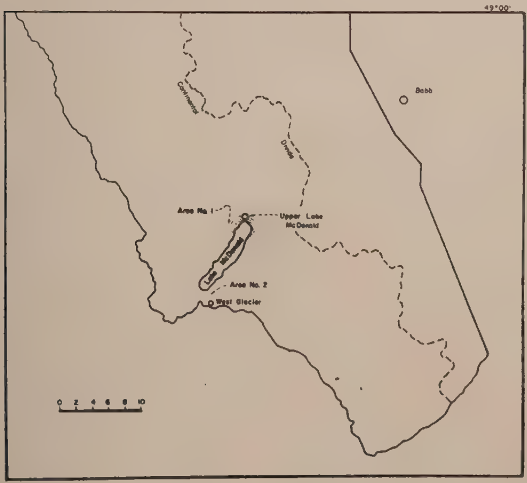

Fig. 1. Map of Glacier National Park with areas studied.

Geology and Soils

The rocks of Glacier National Park are predominantly sedimentary in origin and belong to a single unit known as the Belt series. The area is part of a large geosyncline occupied during the Proterozoic Era by a shallow sea into which sediments of sand and mud were dumped (Dyson 1949). The sedimentary rocks thus formed have undergone considerable metamorphism to produce dolomites, argillites and quartzites (Fenneman 1931). The landscape has been altered perceptibly by Pleistocene glaciers. Huge isolated rocks in the glacier drift are encountered on the slopes above McDonald Lake. In general the soil, except for a shallow surface layer, is rather immature.

Climate

In few places in the Rocky Mountains can one find a greater contrast in climate in so few miles. The east slope of the Park has a distinctly continental climate with moderate to high wind velocities and rather wide temperature extremes, while the area west of the Continental Divide, although about 500 mi. inland from the Pacific Coast, has a semi-maritime climate with moderate to high precipitation and humidity, and relatively lower temperature extremes and wind velocities (Tables I and II).

Climatic conditions at Babb, located near the eastern boundary of the Park 35 mi. northeast of West Glacier are quite typical of the portion of the Park lying east of the Divide.

The mean annual precipitation at West Glacier U.S.W.B. (1935) which lies about 1.5 mi. south of the lower end of Lake McDonald is 26.65 in. April, the driest month, receives an average of 1.47 in. of precipitation with August, March and July in that order receiving only slightly more. The four months with the greatest amount of precipitation are October through January. December, the wettest month, averages 3.24 in. One hundred and six days of each year have .01 in. of precipitation or more. The snowfall at West Glacier averages approximately 119 in. per year. The average number of consecutive frost free days per year is 104.

TABLE I. Precipitation averages for three stations

	Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Babb	1.10	.82	1.10	1.74	2.40	3.06	2.21	1.92	2.24	1.13	.85	.88	19.45
West Glacier	3.05	2.17	1.59	1.47	1.88	2.46	1.76	1.50	2.26	2.64	2.63	3.24	26.65
Upper McDonald Lake	4.24	3.37	1.93	1.28	3.23	3.34	2.06	1.08	2.37	2.31	2.14	3.38	30.73

TABLE II. Temperatures at two stations

	Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Average temperatures													
Babb	17.0	20.0	27.2	37.9	46.2	53.9	60.0	58.4	50.1	42.2	30.7	20.2	38.6
West Glacier	20.2	25.2	32.4	41.8	49.4	57.0	65.5	63.4	53.0	42.6	30.8	21.8	42.0
Average maximum													
Babb	27.1	31.6	38.8	50.6	58.7	67.3	76.1	74.2	63.4	54.4	41.4	31.1	51.2
West Glacier	28.3	35.9	44.4	56.1	64.8	73.5	85.4	82.2	68.1	55.1	39.7	29.7	55.3
Average minimum													
Babb	6.9	8.5	15.7	25.2	33.8	40.5	44.0	42.5	36.8	30.1	20.0	9.4	26.1
West Glacier	12.2	14.6	20.5	27.6	33.9	40.5	45.6	44.7	37.8	30.2	21.9	13.8	28.6

Lowest-highest temperatures

	Jan.	Feb.	Mar.	Apr.	May	June
Babb	−48, 95	−53, 61	−34, 64	− 8, 84	−14, 85	22, 95
West Glacier	−38, 63	−27, 60	−24, 70	21, 82	21, 92	26, 98
	July	Aug.	Sept.	Oct.	Nov.	Dec.
Babb	28, 95	21, 96	− 3, 89	−20, 81	−31, 68	−48, 60
West Glacier	29, 100	31, 99	7, 91	5, 83	−17, 70	−42, 64

The weather data from upper Lake McDonald station are regrettably scanty and not positively typical since they were collected only from 1906-1910. However, because this station is located in the immediate vicinity of area number one of this study, the data insofar as they go, seem quite significant. It should be noted that the mean annual precipitation here is 30.73 in. which is approximately 4 in. greater than at West Glacier.

The nature of the climate is reflected significantly by the vegetation. Fungi, lichens and mosses abound on the rocks, tree trunks and down timber. The moss coverage of the ground in the quadrats averaged more than 50%, in some cases reaching 90 and 100%.

The climate is moist enough to permit the occurrence of some of the climax dominants of the Pacific Coast, e.g., western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* D. Don) and Pacific yew (*Taxus brevifolia* Nutt). It should be added however, that conditions are evidently below optimum for these species; viz. Pacific yew takes the form of a small shrub here instead of the sizeable tree it becomes along the coast. This region represents the easternmost limits of the range of all three of these species. With the possible exception of a reported group of some half-dozen trees of red cedar near the upper end of St. Mary's Lake, these three species do not cross the Continental Divide.

OBJECTIVES

The objectives of this study were to test the assumptions that have been made concerning successional trends in this section of the Northern Rockies, to provide an accurate picture of the actual structure of the forest community at mid altitudes in the area and, where possible, to correlate this with the environmental factors involved.

METHODS

Two distinct areas were chosen for study. The first was on both sides of Lake McDonald near the north end (Fig. 1). This region, according to available records, has not been disturbed by lumbering or fire at least since 1910.

In area No. 1, 100 sample plots ten meters square were laid out, 60 on the east and north of the lake and 40 on the west side. The quadrats were taken in seven different sites distributed to cover an area between 5 and 6 mi. horizontally and 1000 ft vertically, i.e., between 3200 ft and 4200 ft elevation. In each site the quadrats were spaced at 50 meter intervals. All trees in each plot were counted and their diameters at 4 ft above the ground measured, those below one inch DBH (diameter breast height) being listed as seedlings.

The per cent of crown coverage represented by each tree species in the plots was estimated by inspection. All dead trees, including stumps, were noted, tabulated separately (Table III), but included in the statistical treatment. All spermatophytes occuring in the quadrats were identified to species where possible. An estimate was made in each quadrat of the per cent of the ground covered by moss.

Table III. Percentage of total basal area in sq. ft. represented by dead trees

Species	Total BA	BA of dead trees	% BA of dead trees
Thuja plicata	321.53	4.83	1.5
Tsuga heterophylla	286.55	21.88	7.6
Larix occidentalis	242.78	85.73	35.4
Pinus monticola	91.57	24.29	26.5
Pseudotsuga menziesii	78.11	11.74	15.0
Pinus contorta	18.51	2.91	15.7
Abies grandis	11.40	.455	4.0
Betula papyrifera	7.93	2.25	28.4
Picea Engelmanni	7.11	23	3.2

The data presented in Tables III-IV are shown in Figure 2 as phytographs, i.e., polygons formed on four axes representing the criteria which are regarded as most significant in determining the phytosociological position of the tree species in a forest community (Lutz 1930). The four criteria used were (1) relative density, i.e., the number of individuals of a given species represented as a per cent of the total number of individual trees of all species one inch DBH or larger; (2) frequency, i.e., the number of sample plots in which are found one or more individuals of a given species one inch DBH or over and expressed as a per cent of the total number of sample plots; (3) number of size classes by which each species is represented expressed as a percentage of the total of four possible size classes; and (4) the total basal area of each species expressed as a per cent of the combined total basal area of all the trees one inch DBH and over in the 100 quadrats. A fifth value adapted from Merkle (1954), namely, percentage of crown coverage, is represented by a broken line plotted on the basal area radius. In area No. 2, which was devastated by fire in 1929, 20 quadrats ten by ten meters were laid out. Only density and frequency of the tree species were noted here. These data are given in Table V.

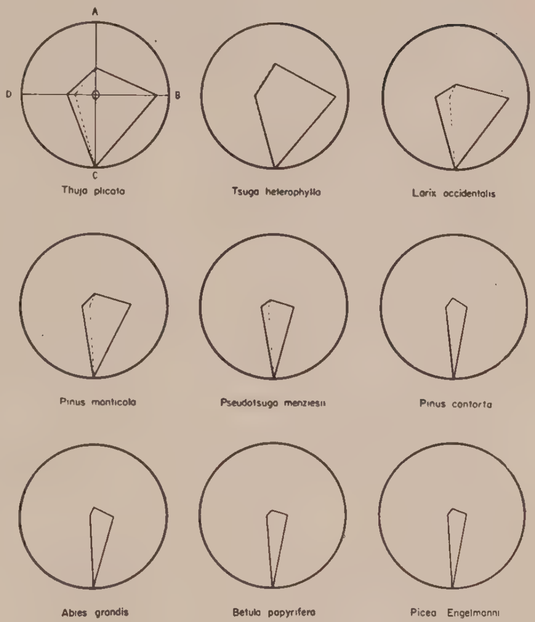

Fig. 2. Phytographs for the tree species in area one. Radius OA represents per cent of total abundance, OB per cent of frequency, OC number of size classes, OD per cent of basal area. The broken line plotted on radius OD represents the per cent of canopy coverage.

Table IV. Number of trees in each size class

Species	Under 1″	1″-3″	3″-10″	Over 10″
Thuja plicata	2,653	292	233	179
Tsuga heterophylla	12,638	392	164	215
Larix occidentalis	27	9	21	160
Pinus monticola	282	46	79	65
Pseudotsuga menziesii	279	22	10	35
Pinus contorta	9	22	32	12
Abies grandis	231	37	28	8
Betula papyrifera	6	6	9	8
Picea Engelmanni	20	20	11	4

Table V. Data from the 20 sample plots in area 2 (burned over in 1929)

Species	Numbers		Frequency	
	1″ & Over	Seedlings	1″ & Over	All sizes
Pinus contorta	642	549	85%	85%
Populus trichocarpa	62	140	70%	75%
Populus tremuloides	38	78	45%	50%
Betula sp.	26	7	35%	40%
Larix occidentalis	21	3	40%	50%
Picea Engelmanni	4	5	10%	30%
Pinus monticola	2	2	15%	20%
Pseudotsuga menziesii	0	5	0%	20%
Tsuga heterophylla	0	1	0%	5%

A total of 26 species of shrubs was noted in area No. 1, 23 of which were found in the sample plots. The 23 are listed below with their frequencies.

Species	Frequency
Vaccinium membranaceum	69
Pachistima myrsinites	45
Berberis aquifolium	42
Rosa gymnocarpa	41
Spiraea lucida	38
Acer glabrum	35
Taxus brevifolia	24
Salix sp.	20
Lonicera sp.	20
Amelanchier alnifolia	10
Vaccinium myrtillus	9
Symphoricarpos occidentalis	9
Rosa sp.	8
Archtostaphylos uva-ursi	7
Eleagnus canadensis	7
Menziesia glabella	7
Vaccinium scoparium	7
Rubus parviflorus	7
Alnus tenuifolia	4
Cornus sericea	1
Sorbus sitchensis	1
Ceanothus velutinus	1
Holodiscus discolor	1

Approximately 46 species of herbaceous angiosperms were identified in quadrats in area No. 1. Those with significantly high frequencies are listed below by families.

	Frequency
Ericaceae	
Chimaphila umbellatum	91%
Pyrola secunda	63%
Pyrola chlorantha	39%
Pyrola asarifolia	35%
Liliaceae	
Clintonia uniflora	89%
Xerophyllum tenax	43%
Orchidaceae	
Goodyera decipiens	80%
Listera convallarioïdes	42%
Caprifoliaceae	
Linnaea borealis	82%
Violaceae	
Viola orbiculata	53%
Compositae	
Hieracium albiflorum	40%
Adenocaulon bicolor	26%
Saxifragaceae	
Tiarella unifoliata	33%

All species sampled in area No. 1 were distributed in frequency classes[1] and compared with Raunkiaer's norms (Oosting 1948) which are shown in parenthesis: class 1—68 (53) %, class 2—13 (14) %, class 3—7 (9) %, class 4—5 (8) % and class 5—6 (16) %. It will be seen that 68% of the species sampled have a frequency between one and 20%, which is higher than Raunkiaer's norm. This indicates that the community has a rather heterogeneous composition.

A study of the data as represented by the phytographs definitely indicated that western hemlock and red cedar are climax dominants. This conclusion is in agreement with the finding in adjacent Northern Idaho by Huberman (1935), who listed these two species with lowland white fir (*Abies grandis* Lindl.) as the climax dominants of that area. Hansen (1948) indicated that western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Dougl.) together cover over 50% of the cedar-hemlock-Douglas fir forest of the Glacier Park region. Area No. 1 of this study certainly does not conform to this pattern. For example, lodgepole pine was found in only 15 of the 100 quadrats and accounted for only 3% of the total number of individual trees. Western larch with a rather high frequency (75%) likewise had the insignificant density of 9.1%. The rather high percentage (23%) of the total basal area accounted for by this species is explained by the fact that it is represented by very large, old trees. Approximately 86% of the total basal area of dead trees was made up of larch. Barring fire or other disturbances in the future this species is expected to decline still further in abundance.

Hansen (1948) concluded from a pollen profile study of two bogs in the area near Lake McDonald that western hemlock probably has not existed in abundance during post-glacial times in Glacier Park. The highest representation of this species (5%) was attained in the upper third of both sections. This is rather surprising when it is noted that hemlock now ranks first in abundance of the tree species. Perhaps this represents a continuation into recent time of the mesic trend that Hansen inferred from the pollen sections.

The total crown coverage of the trees is 76%, which is lower than typical for a mature cedar-hemlock climax forest. This may be explained in part by the considerable number of dead trees (Table III), many of which have not been over-topped by living forms. Also, a very high percentage of the trees are relatively young (66% less than 10 in. DBH).

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[1] Class 1 includes species with frequencies from 1- 20%
Class 2 includes species with frequencies from 21- 40%
Class 3 includes species with frequencies from 41- 60%
Class 4 includes species with frequencies from 61- 80%
Class 5 includes species with frequencies from 81-100%

Zonation is rather apparent in area No. 1. Western red cedar was confined almost entirely to the 3200-3800 ft zone. In the eight quadrats between 3800 ft and 4200 ft no cedar occurred, and in nine quadrats between 4300 ft and 4500 ft (which were not included in the statistical study) cedar was present in only two. The pattern for hemlock was very similar. The frequency of spruce showed a positive correlation with altitude, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) was confined to two quadrats both of which were above 4000 ft.

Area No. 2 is covered with a stand of young timber characterized by three post-fire seral dominants occurring in significantly high numbers. Listed in the order of their abundance they are lodgepole pine, black cottonwood (*Populus trichocarpa* T. & G.) and quaking aspen (*Populus tremuloides* Michx.). Although in the Rocky Mountain area aspen is regarded as the deciduous tree most commonly found in an area following a fire (Weaver & Clements 1938, Oosting 1956), it is interesting to note that in this region it is surpassed both in frequency and abundance by black cottonwood. The latter was not noted in the undisturbed coniferous stands, so is apparently unable to persist except in low flat meadows and along lake shores.

SUMMARY

During the summer of 1953, a study was made of the composition of the cedar-hemlock forest around Lake McDonald in Glacier National Park, Montana. The region surveyed was arbitrarily restricted to elevations between 3200 and 4200 ft.

Two areas were analyzed, one an undisturbed forest and a second which had been severely burned over in 1929. One hundred quadrats of 100 sq. m. size were taken in the former and 20 in the latter. Phytographs present relative density, frequency, size classes, basal area, and crown cover for each tree species. Only frequency was tabulated for the shrubs and herbaceous plants.

Ten species of trees, 26 shrubs and 60 herbaceous plants were found. *Thuja plicata* (western red cedar) and *Tsuga heterophylla* (western hemlock) were clearly climax dominants, with *Abies grandis* (lowland white fir) and possibly *Pseudotsuga menziesii* (Douglas fir) codominants of much less importance. *Larix occidentalis* (western larch) and *Pinus monticola* (western white pine) appeared in the role of pyric subclimax species. Six species of shrubs (*Vaccinium membranaceum, Pachistima myrsinites, Berberis aquifolium, Rosa gymocarpa, Spiraea lucida* and *Acer glabrum*) were quite characteristic of the community with frequencies ranging from 69% to 35%. Thirteen herbaceous species distributed among seven families had frequencies of 33% to 91%. Four of these were ericads. Six were very characteristic of the community and are listed with their frequencies: *Chimaphila umbellatum* 91%, *Clintonia uniflora* 89%, *Linnaea borealis* 82%, *Goodyera decipiens* 80%, *Pyrola secunda* 63%, and *Viola orbiculata* 53%.

In the burn area three trees, *Pinus contorta, Populus trichocarpa,* and *Populus tremuloides* predominated in abundance and frequency in the order listed.

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ORGANIC PRODUCTION AND TURNOVER IN OLD FIELD SUCCESSION*

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The establishment of the AEC Savannah River Plant (hereafter designated as the SRP) in Aiken and Barnwell counties, South Carolina, has provided an unusual opportunity for studies on secondary succession. During 1951-52 the approximately 6,000 human inhabitants moved out of an area of 315 square miles to make way for the establishment of the SRP; the entire area was then closed to the public. At that time about 67,000 acres (one-third of the land area) were in croplands and pastures, cotton and corn being the chief crops. From 1952, the first growing season following the cessation of agriculture, to the present time a faculty-graduate student team from the University of Georgia has been engaged in a series of ecological studies on fields of various soil types and locations within the SRP reservation. We have been especially interested in the pattern of metabolism of the "old-field ecosystem" as a whole, the energy flow characteristics of major component populations, and in the role which these components play in the fate of radioactive isotopes experimentally introduced into the ecosystem.

Secondary succession on abandoned cropland has been described for a number of localities in southeastern United States (Oosting 1942, Kurz 1944, Bronck and Penfound 1945, Quarterman 1957). The most complete description is that of Oosting who tabulated the density and frequency of plants in a large series of fields and forests of various ages on the Piedmont of North Carolina. Our studies on secondary succession involve an entirely different approach from that of Oosting and other investigators cited above in that the functional rather than the descriptive aspect is being emphasized. Essentially, we are attempting to measure the energy flow through the different communities which develop on abandoned agricultural land, and thereby to investigate the fundamental relationships between energy and succession. In this paper we are concerned primarily with that part of the energy flow which constitutes the net primary production (i.e. apparent photosynthesis or total photosynthesis minus plant respiration), and secondarily with the overall heterotrophic utilization of the annual net production of the producers. That portion of the energy flow of the community which constitutes the respiration of the producers as well as the details of energy flow through consumer levels will be considered in other papers. The time period of primary consideration in this paper is the first five to seven years of succession, which essentially covers the period when annuals and biennials are dominant.

Methods

The method of measuring net primary production is illustrated in Table I. At approximately one month intervals during the growing season all plants were removed from a series of one square meter quadrats. The generally sandy soils of the area and the shallow rooted growth form of early seral species made it easy to pull up plants with little loss of root material. Each species was placed in a separate paper bag and taken to the laboratory where the number and dry weight of each species was determined. In a number of cases soil was sifted after the plants had been pulled up to obtain an estimate of the rootlets not included in the harvest, but the amount of material obtained in this way was not large enough, nor variable enough, to warrant laborious sifting on a routine basis. The total weights of each species were tabulated as shown in Table I, thus providing an estimate of the standing crop at any one time as well as a basis for calculating the net production. The maximum weight of each species was listed in the final column and these values summed to provide the estimate of the annual net production. For annuals the entire weight of the plants (shoots and roots) was included. For perennials only the new growth was included since part of the weight of perennial species represents production from a previous year. Almost all of the important species in the old fields during the first few years were annuals, thus simplifying the procedure.

Sampling problems were minimal because the generally level topography and the sandy soils made homogeneous by years of "row crop" agriculture resulted in a relatively uniform post-agricultural vegetation. Since the objective of the study was to measure the rate of change in a given area rather than to describe in great detail the standing crop at any one time, harvest quadrats were spaced 25 feet apart along a transect. Suc-

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TABLE I. Seasonal change in standing crop of green plants in a 3-year abandoned field and calculation of total productivity uncorrected for animal consumption. (Field 3-412, 1954). Figures in grams dry biomass per square meter

Species	April	May	June	July	Aug.	Sept.	Net Production
Rumex........	19.0	0.7	1.6	1.4			19.0
Linaria........	1.2	0.1					1.2
Oenothera......	3.0	3.4	1.2				3.4
Specularis......	3.2	3.3					3.3
Festuca........	0.5	0.3	0.2		0.2	0.1	0.5
Gnaphalium ob..	4.8	20.3	13.4	33.9	28.2	0.3	33.9
Lepidium......		1.3	2.8	2.0	1.5		2.8
Cyperus.......	1.4	2.8	4.2	16.8	18.1	19.2	19.2
Leptilon.......			4.3	11.1	16.0	20.4	20.4
Heterotheca.....	0.6	3.0	8.8	11.9	32.0	50.0	50.0
Haplopappus...	0.4	3.8	18.5	27.7	85.0	110.4	110.4
Miscellaneous species.....	2.5	0.3	1.2	1.3	2.1	2.1	5.9
Totals.........	36.6	39.3	56.2	106 1	183.1	202.5	270.0

cessive samples were taken immediately adjacent to quadrats harvested during the previous month so that the same combinations of locations were sampled at each period. Species-area curves (Oosting 1956, Goodall 1952) indicated that 10 quadarts provided an adequate sample during the first 2 or 3 years of natural succession; with the increase in species diversity in later years it was necessary to increase the number to 20 or more in some cases.

It is important to emphasize that harvests should be made at frequent intervals if a reasonable estimate of production is to be obtained. Note (Table I) that the annual net production is always greater than the standing crop at any one time since not all species in the community reach their maximum growth at the same time (as might, for example, a cultivated crop). As will be emphasized later, standing crop becomes less and less a measure of productivity as succession proceeds.

The estimates of net primary production are to be considered minimal since growth which may have died and become detached from the plant or eaten by animals within a sample interval would not be included. Our studies indicate that such losses within a month interval are small in so far as the old-field type of ecosystem is concerned. Losses to the litter as estimated by changes in litter weights proved to be quite small for the time interval considered, while immediate consumption by herbivores was likewise small. Most consumption was delayed until the organic production was in the form of seeds and detritus. Large mammalian grazers were absent from the areas studied (wild pigs and deer are a factor in some parts of SRP area but not in the areas selected for study). The two common rodents (Peromyscus and Mus) eat some vegetation but are primarily seed and insect eaters. Rabbits and cotton rats (Sigmodon), important herbivores in later stages of succession, were of little importance in the early stages of succession. All the birds are either seed or insect consumers. Insect herbivores were the chief consumers of living plants but population size was small in undisturbed old-fields (Cross 1956). When our energy flow analyses of consumer populations have been completed we expect to be able to estimate the total consumption with some degree of precision. At present we can say that in the early stages of succession consumption of living plants within any one 30-day period is certainly less than 10% and probably less than 5% of the net production (for that period). Consequently, it is feasible to use a "short-term harvest method" for estimation of productivity in a system characterized by delayed heterotrophic utilization of the net primary production. In summary, what we are discussing in this paper is "net community production," that is, organic production in excess of that consumed by the community over short intervals of time. In the early stages of old-field succession such net community production closely approximates true net primary production.

At the time that harvests of living plants were made all of the litter materials, including dead plant material on the surface of the ground as well as the "standing dead," were removed from the quadrat, placed in a bag, and the dry weight later determined. In other words the term "litter" as used in this paper refers to all of the dead plant material above the surface of the soil. During the first several years of succession it was possible to separate out major dominant species from the litter and thus to estimate the rate of decomposition of individual species.

During the autumn of 1951, the cultivated crop or other vegetation in about 600 fields widely scattered over the SRP area was recorded on overlays attached to sectional areal photographs. Each field was given a number and prefixed with another number referring to the map section (for example, 9-111 is field 111 located on map section 9). A set of the maps and overlays are on file both at SRP and at the University of Georgia. These reference fields were visited periodically during the years and were useful in establishing the general pattern of succession in relation to broad soil types. In those fields selected for quantitative study, soil samples from the top 6 in.

and from the 18-24 in. level (A_2 or B horizon) were taken. Determinations of nutrient and organic matter levels, pH, exchange capacity, and texture were made by the Soils Laboratory of the University of Georgia. Additional mechanical analyses employing the Boyoucous hydrometer method were made in our Ecological Laboratory when it became apparent that the silt-clay fraction was a key to the ecology of the fields. The Boyoucous method works well for coastal plain soils which are easily dispersed with hexametaphosphate (Calgon). Excellent data on rainfall and temperatures were available from the 6 weather stations which are being maintained in different parts of the SRP reservation.

Two large fields, 9-111 and 3-412, were selected for an especially intensive analysis. Net production in these two fields, which represent two of the common soil types of the area, have been made each year since the beginning of the study in 1952. Likewise, studies of major animal populations in these fields have been made by various graduate student members of the research team.

Shortly after the establishment of the SRP an extensive program of pine tree planting was begun by the U. S. Forest Service. Pines, of course, are a part of natural succession and would eventually invade the fields. However, because of the very large size of many fields, the raw soil conditions and the frequent absence of a natural seed source, natural reforestation would be slow; hence artificial reforestation was economically desirable. By 1957 most of the original 600 reference fields had been planted, but the special study fields have been reserved and will not be artifically planted. There has been very little invasion of woody plants in these large fields during the first 7 years.

ACKNOWLEDGMENTS

Two "generations" of graduate students have helped in the productivity studies while at the same time carrying out their own independent research. Edward J. Kuenzler, William H. Cross, Leslie B. Davenport, and Robert Pearson contributed much time and energy taking the monthly samples during the first 3 years of the study while Clyde E. Connell, Larry D. Caldwell, Wallace Tarpley, John B. Gentry, and William K. Willard were active during the next several years. Dr. Robert A. Norris took a special interest in the work during 1956-58 when he was Resident Ecologist on SRP. He revisited many of the original reference fields and did some special mapping during the period when the diversity of species was increasing. Dr. Wilbur Duncan, Department of Botany of the University of Georgia, has checked numerous identifications for us. We are, also, indebted to John P. Hatcher, Project Forester for SRP, and his staff for helping out in numerous ways. Finally, Karl Herde, Chief, Radiation Protection Branch of SRP, not only cheerfully made the necessary arrangements for us to work in complete freedom within the area but he, also, took an interest in all the studies and often accompanied us into the field.

PHYSIOGRAPHY AND SOILS OF THE SRP AREA

The SRP area is located on the Upper Coastal Plain physiographic province in Aiken, Barnwell and (to a small extent) Allendale counties, South Carolina. The area borders the Savannah River for about 27 miles; it is about 150 river miles from the ocean, and 14 airline miles downstream from Augusta, Georgia, on the edge of the Piedmont Plateau. As shown in Figure 1 two distinct physiographic subregions are represented, namely,

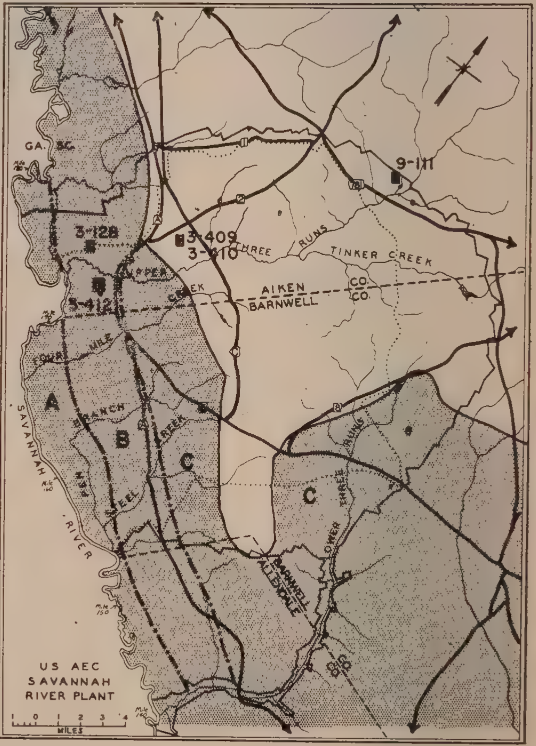

FIG. 1. The AEC Savannah River Plant reservation showing principal streams, highways (A, B, C, 1, 2, etc.), physiographic subregions and location of special study fields (9—111, 3—409, 3—410, 3—128 and 3—412). The shaded area is the Coastal Terraces subregion and the unshaded area the Aiken Plateau or "sandhills" subregion. Three terraces are recognizable as follows: A—Wicomico; B—Sunderland; C—Brandywine.

Table II. Characteristics of major soil types of SRP old-fields

Soil Type	Number of Fields		Nutrients-pounds Per Acre						% Organic	Texture %		
			pH	NO_3	P_2O_5	K_2O	CaO	MgO		Sand	Silt	Clay
Lakeland Sand (Deep phase)	4	A_p	5.7	5	37	27	288	8	1.07	92	5	3
		A_2	5.3	5	5	16	200	5	.15	91	5	4
Lakeland Sand	8	A_p	5.7	9	77	43	451	3	1.10	91	5	4
		A_2	5.3	6	5	7	108	2	0.12	86	6	8
Kalmia Sand-Loamy-Sand	7	A_p	5.8	5	55	42	413	5	0.98	89	6	5
		A_2	5.6	2	6	16	450	3	0.11	87	7	6
Norfolk Loamy-Sand	2	A_p	5.8	10	75	60	500	10	1.45	88	7	5
		B_1	5.4	5	20	10	250	10	0.32	78	5	17
Ruston Loamy-Sand	3	A_p	5.7	5	27	36	683	23	1.00	91	5	4
		B_1	5.2	5	5	54	350	10	0.20	78	8	14
Cahaba Loamy-Sand	3	A_p	6.6		197	202	2100	52	2.04	80	9	11
		B_1	6.3		132	104	1500	50	0.55	75	7	18
Myatt Sandy-loam	1	A_p	5.4	60	15	5	850	T	4.10	60	13	27
		B_1	6.5	10	20	5	850	T	1.14	42	12	46
Izagora Sandy-loam	2	A_p	5.1	5	12	35	300	5	2.97	72	23	5
		B_1	—	—	—	—	—	—	—	52	16	32

Cation Exchange Capacity (in millequivelents cations):—
Lakeland Sand (1 field) A_p=3.05; A_2=1.25.
Norfolk Loamy-Sand (1 field) A_p=3.75; B_1=2.20.
Cahaba Loamy-Sand (2 fields) A_p=4.10; B_1= 2.75.
Izagora Sandy-Loam (1 field) A_p=8.49; B_1=2.70.

the pleistocene Coastal Terraces (below 270 feet elevation) and the Aiken Plateau (above the 270 foot contour). At least 3 terraces are recognizable within the former subregion as shown in Figure 1. The lowest terrace (Wicomico) is the present very broad Savannah River floodplain which is covered with dense swamp forest. The higher terraces have a level to gently rolling topography and were intensively cultivated where drainage and soils were favorable. The Aiken Plateau is relatively hilly and deeply dissected by small streams. There are extensive areas of "sand hill" vegetation of scrub oak and long-leaf pine forests along the ridges and many of the farms in this region were small and marginal in agricultural productivity. The geology and physiography of the South Carolina Coastal Plain has been well described by Cooke (1936).

As is characteristic of the "geologically young" Coastal Plain in general, soil profiles on the SRP area are "immature," and a large number of different soil types have been delimited. Small differences in elevation, drainage and parent material may produce striking differences in color, texture, organic content and other characteristics, so that distinct soil types may exist side by side in an area which might at first appear to be uniform. Sixty-three soil types have been described from the Edisto Soil Conservation District which includes the SRP according to a list furnished by P. W. Montgomery, State Soil Scientist of South Carolina. However, only a few of these are important agricultural soils and hence of primary interest in the study of old-field succession. Well-drained to moderately well-drained soils which were most widely used for the standard crops of the area (cotton, corn, peanuts, peas, watermelons, etc.) fall largely into 5 series as follows: the Lakeland and Ruston series of the Aiken Plateau and the Kalmia, Norfolk and Cahaba series of the Terraces. Poorly drained soils of the Myatt and Izagora series were also cultivated to a limited extent. Fields representative of all 7 of these series have been included in our studies. Characteristics of the major soil types in the 30 special study fields are summarized in Table II, while complete profile descriptions of the two major study areas and also of two other fields of contrasting soil types are shown in Table III.

In most of the soils cultivated prior to the establishment of SRP the topsoil or A_p horizon (i.e. "plowed" layer) is 6-18 in. thick, ranges in color from light to dark gray, and in texture from 60% to 95% sand. The subsoil, which technically is the A_2 horizon in very sandy types and the B horizon in heavier soils, is usually sharply marked off and brightly colored yellow or red in well drained situations. The Myatt and Izagora soils

TABLE III. Profile descriptions of soils of four SRP fields

Field Number & Soil Type	Horizon	Depth lower edge (inches)	Color	Structure	Texture % Sand-silt-clay
9-111 Lakeland Sand	A_p	8	grayish-brown	weak medium crumb	89— 5—6
	A_2	38	yellowish-brown	weak medium crumb	86— 8— 6
	B_1	(very narrow and weakly developed)			
	B_2	70	yellowish-red	weak medium sub-angular blocky	70— 4—26
	C	—	red mottled with yellow		
3-412 Cahaba Loamy-Sand	A_p	12	dark gray brown	weak medium crumb	85— 7— 8
	B_1	15	dark red-brown	weak medium crumb	80— 5—15
	B_2	60	yellowish-red	weak medium crumb	81— 4—15
	C	—	reddish-yellow	weak medium crumb with some quartz gravel	83— 3—14
3-409 Lakeland Sand (deep phase)	A_p	6	light olive gray	weak medium crumb	94— 3— 3
	A_2	24	pale yellow	weak medium crumb	92— 3— 5
	A_3	60	yellow	weak medium granular	85— 7— 8
	B_1	Not developed			
	B_2	66	yellow	weak medium granular	70—12—18
	C	—	red mottled with yellow	sandy clay	53—10—37
3-410 Ruston Loamy-Sand	A_p	12	brownish-gray	weak crumb	89— 6— 5
	B_1	42	yellowish-red	weak sub-angular	79— 8—13
	B_2	84	red	sub-angular, blocky	61— 3—36
	C	—	red	sub-angular, blocky	65— 2—33

* Field descriptions made by P. W. Montgomery assisted by P. Wakefield. Textural analyses made in the University of Georgia Ecological Laboratory by E. W. Kuenzler.

have a white to bluish clayey B horizon. The agricultural soils fall naturally into three groups: (1) the "yellow sands," light sandy soils with a yellow subsoil, and including the Lakeland, Kalmia and Norfolk types, (2) the "red sands," somewhat heavier soils with orange or red subsoils and including the Ruston and Cahaba types, and (3) the poorly-drained soils with wet, heavy subsoils and including the Myatt, Izàgora and other types. All of these soils have a low pH and a relatively low content of organic matter.

The texture of the soil, and especially the texture of the subsoil, has proved to be a key factor in the ecology of the communities which have developed on the former agricultural land. The amount of clay and silt in the subsoil largely controls the water and nutrient holding capacities of the soil as a whole and thereby the availability of water and nutrients to the plants. The series of soil types as listed in Table II actually forms a gradient from the lightest and driest soils to the wettest and heaviest soils that were used in ordinary "row crop" agriculture. The nutrient and organic matter levels listed in Table II are based on analyses made during the first year of the study. As shown in Table IV there has been a tendency in the lighter soils for phosphorus, calcium and organic matter to leach downward. Thus, 3 years after the end of cultivation these materials had decreased in the topsoil and increased in the subsoil, on the average.

THE GENERAL PATTERN OF SUCCESSION

A check-list of the most important plants of the early stages of old-field succession is found in the Appendix. In this paper dominance (i.e. importance in the community) is considered in terms of the net production of dry matter and not in terms of the number or height of individuals. A dominant, for our purposes, is arbitrarily defined as any species producing one gram or more of dry matter per square meter per growing season irrespective of the time in the year when it was produced. Species producing less than one gram were placed in a miscellaneous category and not listed separately in the tables that follow. Although many genera were represented by several species in the fields, usually only one species in a genus was important enough productivity-wise at any one time or place to be a dominant by the above definition. Consequently in the discussions and tables that follow, the genus name suffices to designate the species in many cases.

The changes which occurred in field 9-111 as shown in Table V illustrate the general pattern of succession in relation to net production on the well-drained soils. Woody forbs were major dominants during the first 5 years or so, with horseweed (*Leptilon canadense*), yellow aster (*Haplopappus divaricatus*) and camphorweed (*Heterotheca subaxillaris*) usually appearing in that order. The growth form of these three forbs is illustrated in the photograph of Figure 2. Leptilon was al-

TABLE IV. Soil nutrient levels in December 1951 (last year of cultivation) and in December 1954 (after three years of natural succession). (Figures are in pounds per acre; T = trace)

Field No.	Crop in 1951	Soil Horizon	P_2O_5		K_2O		CaO		% Organic	
			1951	1954	1951	1954	1951	1954	1951	1954
5-146 Kalmia loamy-sand	Cotton	A_p	40	45	40	44	700	200	0.92	0.69
		A_2	T	18	T	22	100	600	0.08	0.19
2-105 Lakeland loamy-sand	Cotton	A_p	150	70	65	36	850	300	1.18	0.80
		A_2	T	9	50	20	100	200	0.69	0.22
9-111 Lakeland sand	Corn	A_p	70	20	T	28	550	200	1.31	1.00
		A_2	T	10	40	24	300	200	0.17	0.22
9-112 Lakeland sand	Cotton	A_p	180	18	50	18	300	300	1.07	0.80
		A_2	T	3	T	24	50	200	0.26	0.19
1-392 Izagora loamy-sand	Peanuts	A_p	T	17	T	30	100	100	0.88	0.80
		A_2	10	10	T	14	100	400	0.17	0.19
5-150 Kalmia sand	Corn	A_p	65	63	25	16	1100	100	1.18	0.58
		A_2	T	19	T	12	200	50	0.10	0.43
Averages		A_p	84	39	30	29	600	200	1.09	0.79
		A_2	2	12	15	19	142	275	0.24	0.24
Totals both horizons			86	51	45	48	742	475	1.33	1.03

TABLE V. Net Primary Productivity (gms dry wt/m²/year) of Field 9-111

Species	YEARS ABANDONED			
	1 (1952)	2 (1953)	3 (1954)	5 (1956)
Linaria	18.3			
Leptilon	352.6	39 6	1 1	0.3
Gnaphalium purpureum	1.6	2.2	7.8	11.0
G. obtusifolium	41.6		6.3	45.5
Digitaria	74 9			6 1
Rumex		3.9	4.4	29 6
Lechea		111 2	94 9	18.3
Hypericum		19 5	59.8	33.2
Oenothara		0 8	8.1	1.5
Cyperus		0.4		0.7
Haplopappus		149 0	24 2	72.2
Specularia			1 3	
Lepidium			3 2	.4
Andropogon			1.4	16.7
Festuca			15 8	.3
Eragrostis			44 52	
Diodea				14.1
Heterotheca				14.4
Triplasis				21 4
Leptoloma				3.4
Miscellaneous	4 9	5.1	21.1	16.1
Totals	494.0	331.7	282.9	308.6
Number of dominant species	5	6	13	15

most always by far the main producer during the first growing season. By late September of the first year these tall weeds often reached 6 feet or more in height and formed dense, uniform stands. Crabgrass (Digitaria) frequently formed an understory and usually was the second most important species productivity-wise. During the second and subsequent years Leptilon was invariably present in the study fields but always in a stunted form (two feet high or less). Although the number of individuals per m² was often greater in these years the contribution of the species to total net production declined rapidly as shown in Table V. Yellow aster (*Haplopappus divaricatus*) replaced horseweed as the major dominant during the second year in most cases. Tall, uni-

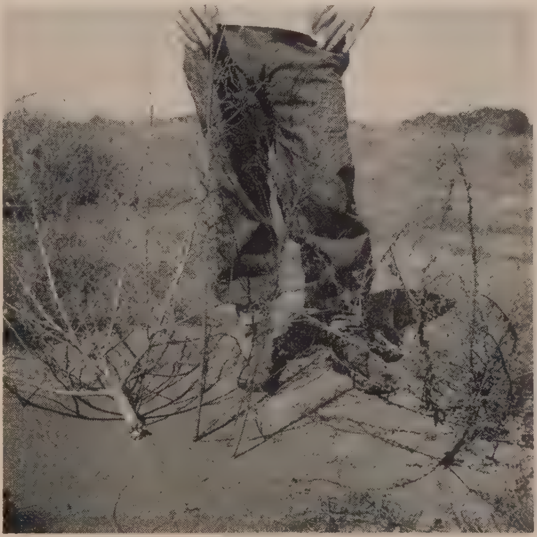

FIG. 2. The growth form of three major forb dominants. From left to right: *Heterotheca subaxillaris* (individual from previous growing season), *Haplopappus divaricatus* (held by hand of observer), *Leptilon canadense* (partly dwarfed 2nd year individual), and *Heterotheca* (individual from current season).

form stands of this species were quite spectacular when the yellow flowers were at their peak in September and October. Figure 3a shows a typical stand of Haplopappus on a fertile area (Field 3-412) as it appeared in the winter of the second year of abandonment when the stalks were bare of leaves. The yellow aster continued to be an important dominant during the third and fourth years, and in some fields was still important after 7 years. As shown in Table V the number of dominants increased with time; after the second year there was never a clear-cut dominance by one or two species. Field 9-111 was atypical in that Lechea was prominant; in most other fields of the Lakeland soil series, or other well-drained types this plant was only a minor component. Also, Heterotheca was less important in field 9-111 than in most other fields. In field 3-412, for example, it became a major dominant by the third year (Table I) and continued important in subsequent years. It is important to note that the Coastal Plain species of Heterotheca (i.e., *H. subaxillaris*) is quite different in growth form and seral position as compared with the Piedmont species, *Heterotheca latifolia,* which has recently been described as replacing horseweed as a first year dominant in abandoned croplands in some areas (Keever 1955).

During the spring of the first growing season blue toadflax (Linaria) often formed a conspicuous blue carpet for a brief period, but these small plants made only a small contribution to total annual production. Rumex and *Gnaphalium purpureum* along with many other species were conspicuous during the spring and early summer of later years. From the third to the fifth or sixth year the large *Gnaphalium obtusifolium* often was a midsummer dominant and a major contributor to the annual production. In fact, the general pattern was one of change from a single crop of plants maturing in the fall, as was characteristic during the first two years, to three distinct seasonal crops maturing in spring, mid-summer and fall, as occurred in subsequent years. In Table I species forming these 3 crops in field 3-412 during the third year are grouped together. As will be discussed later the general pattern of succession resulted in greatly increased species diversity, a change in the seasonal distribution of production, a decline in the size of the terminal or fall standing crop, but not much change in total annual production (see also Fig. 3).

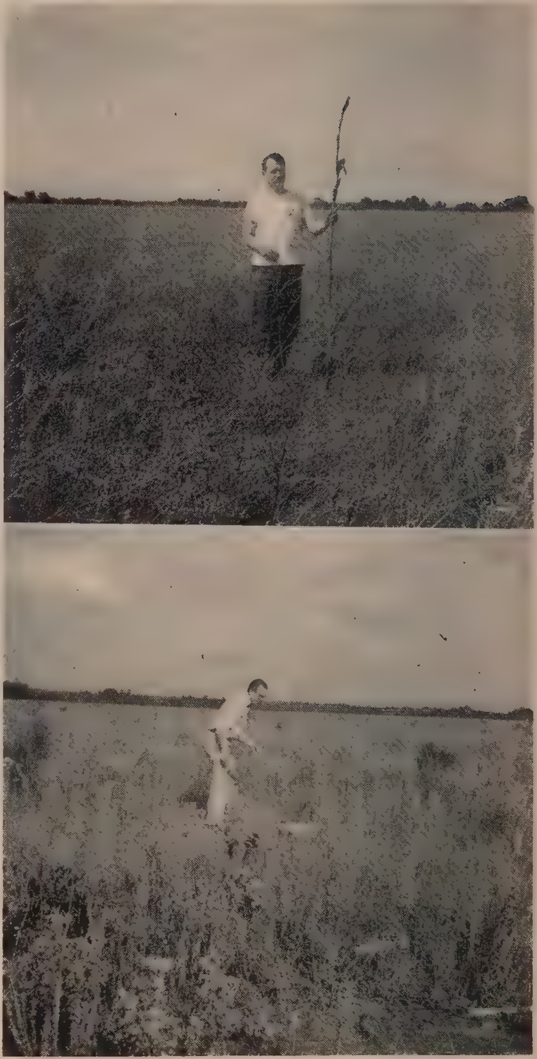

Fig. 3. Field 3—412 as it appeared at the end of the second growing season (1953) and at the end of the fifth season (1956). Vegetation during the second year (Fig. 3a, upper photograph) consisted of an almost pure stand of Haplopappus, many individuals of which were almost as tall as the corn which had been previously grown in the field (1951). By the fifth year (Fig. 3b, lower photograph) the number of species was much greater and the height of the forbs much less, and there were no clear-cut dominance by any one or two species. The perennial Eupatorium (dark clumps) and Andropogon (light colored clumps in the background) were beginning to appear as widely scattered clumps in the matrix of annuals and biennials.

Broomsedge (Andropogon), a bunch grass destined eventually to become the major dominant of the perennial herbaceous stage which follows the annual "weed" stage and which precedes the invasion of shrubs and trees, appeared in many fields by the third year. However, Andropogon did not become important until about the fifth or sixth year when scattered clumps became noticeable (Figure 3b). By the eighth year broomsedge formed a closed stand only in certain small fields on heavier soil types, or locally in the large fields. In contrast to the one-species-per-genus of the forb dominants, the two common species of the genus Andropogon (*A. virginicus* and *A. ternarius*) appeared in equal abundance or in various ratios while one or more of three rarer species (*A. scoparius, glomeratus,* and *Elliottii*) sometimes showed local dominance. The factors affecting broomsedge invasion and the functional aspects of the broomsedge community will be considered in more detail in later papers.

As would be expected soil type greatly influenced the pattern of succession. Certain well-marked deviations from the above described pattern were associated with the more extreme soil types. The contrast during the first two years between the well-drained and poorly-drained types is shown in Table VI. While the annual productivity of these two particular fields was similar (the relation of soil type to productivity will be considered in a subsequent section), the distribution of productivity by species was different. In the poorly-drained field, the number of dominants was greater. Leptilon was much less important, and Haplopappus and Heterotheca were important in the first and second years respectively in contrast to a later dominance in the well-drained soil types.

Table VI. Comparison of species composition and net production (gms. dry matter/m^2/year) during the first two years of secondary succession on the extreme soil types used for row-crops (cotton and corn) prior to 1952

Field Number	9-111		3-128	
Soil Type	Lakeland Sand (well drained upland type)		Izagora Sandy-loam (poorly drained lowland type)	
% Silt-Clay Topsoil	10		31	
Subsoil	13		58	
Species	First Year (1952)	Second Year (1953)	First Year (1952)	Second Year (1953)
Linaria	18		9	
Leptilon	353	40	83	9
Gnaphalium purpureum	2	2	5	3
G. obtusifolium	4		5	25
Digitaria	75		150	
Rumex		4	5	10
Lechea		111		
Hypericum		20	7	36
Oenothera		1		1
Cyperus		1	53	50
Haplopappus		149	86	71
Cynodon			9	66
Diodia			9	5
Polypremum				21
Heterotheca				75
Others	3	1	5	2
Total Net Production	494	331	425	374
Number dominant species	5	6	12	12

The effect of soil type on species composition is shown more broadly in Table VII which summarizes the average terminal standing crop during the second and third years in a series of 19 fields arranged in a gradient from the dry sands to the wet silt-clay types. In general, the number of dominants and the speed of succession increases with increasing silt-clay percentage and/or nearness of the water table to the surface. Thus, Cyperus, perennial grasses such as Cynodon and Andropogon, and the woody perennials Eupatorium, Bignonia and Rubus invade the heavier or less well-drained soils more rapidly than they do the well-drained light soils. At the other extreme, in deep sands, the annual forb stages (i.e. Leptilon, Haplopappus, Heterotheca) tend gradually to give way to a stand of sand-hill grasses of the genera Aristida, Leptoloma, Panicum and others. Diodia was also usually more prominent in the lighter soils.

To summarize, the vegetation, especially the autumn aspect, appeared much the same during the first year regardless of the soil type, except that Haplopappus shared dominance with Leptilon in poorly drained sitautions. During the second and third years species composition began to show marked differences on different soil types, and the divergence increased during the next several years. Thus, by the third or fourth year one could identify the soil type and estimate approximately the silt-clay percentage of the subsoil from the composition of the vegetation. Part of the divergence in species composition resulted from a difference in the rate of succession (many species appearing sooner on the heavier soils as compared with the lighter ones), and part was the result of the virtual restriction of certain species to specific soil series (*Aristida tuberculosa* on deep sands or Polypremum on wet soils, for example). Thus, relative rates of succession can serve as ecological indicators of soil differences as well as specific species of plants which have a high "fidelity" for a particular condition.

The general pattern of upland old-field succession on SRP resembled that described by Oosting (1942) for the lower edge of the Piedmont Plateau in that the general sequence of life forms was similar (annual forbs to perennial grasses), and in that Leptilon was a major dominant during the first year. Succession on SRP differed from that of the Piedmont in the following respects: (1) The yellow-flowered Haplopappus and Heterotheca replaced the white aster (*Aster pilosus*) as second and third year dominants. (2) Ragweed (Ambrosia), often an important early seral dominant on the Piedmont, was generally absent on the uplands of SRP although of importance in some lowland fields (Table

TABLE VII. Effect of soil type and drainage on the terminal standing crop during second and third years of abandonment (1953-1954) as indicated by the grams of average dry biomass per square meter

Soil type:	Lakeland deep phase	Lakeland	Ruston	Cahaba	Kalmia	Myatt and Izagora
Physiographic subregion:	Plateau	Plateau	Plateau	Terrace	Terrace	Both
Drainage:	Extreme	Excellent	Excellent	Good	Moderate	Poor
% silt-clay in subsoil:	9	14	22	20	12	44
Number of fields:	3	3	3	3	4	3
A. OVERSTORY FORBS						
Haplopappus	38.6	96.8	30.6	247.4	102.9	39.4
Heterotheca	21.7	16.8	69.8	21.6	6.2	22.5
Leptilon		21.9	0.2	13.8	0.8	3.6
Lechea		21.7				
Gnaphalium ob.		3.1		0.5	13.8	
Eupatorium			40.0			
Ambrosia					9.0	
Bignonia					17.7	13.3
Rubus					28.0	30.5
Erigeron						23.5
B. UNDERSTORY FORBS AND SEDGES						
Hypericum	1.4	44.7	1.0	0.7	9.6	14.4
Diodia	38.1	5.1	3.9		8.6	1.6
Cyperus	0.2	0.3		6.6	55.1	3.1
Lespedeza	1.3	1.6		0.5	2.7	13.5
Polypremum					2.1	14.6
Cassia					0.4	1.0
C. GRASSES						
Aristida	21.7					
Leptoloma	14.2					
Cynodon	10.0	3.8	148.1			127.8
Digitaria				1.2	5.5	0.5
Andropogon		0.5	4.0	0.4		5.5
D. OTHERS	4.1	5.6	4.5	4.0	3.4	5.4
Totals	151.3	221.9	302.1	296.7	265.8	320.2
Number major Dominants	8	9	7	5	12	14

VII). (3) The rate of succession was slower and the annual and biennial forb stages lasted longer, especially on the light soils. For example, Oosting found that Andropogon rapidly invaded the clay Piedmont soils and established major dominance in 3 or 4 years in contrast to 6-8 years required for similar dominance on SRP. (4) The invasion of pines was very much slower, partly the result of the sandy soils and partly the result of the much greater average size of SRP fields and consequent greater distance from a seed source. The pattern of succession on some of the lowland SRP fields most nearly resembled Oosting's Piedmont fields, which is not surprising since the clay content of some of these fields approaches that of the Upland Piedmont, and since the climate of the lower Piedmont is not greatly different from that of the adjacent Upper Coastal Plain.

NET PRODUCTION AND SUCCESSION

Total annual net production of dry matter in the two intensive study fields for the first 7 years of succession is shown in Figure 4. Rainfall for each year and for each growing season is also shown. Temperatures during the seven years did not deviate more than 3° F from the average 10 year record of the SRP stations. As far as we could determine, temperature was not a major factor in bringing about annual differences in production rates during the period of study.

The trends in the two fields were quite similar, with production averaging greater in field 3-412 where soils were somewhat more fertile (Tables II and IV). In both fields production was much the greatest during the first year, declined in the second year, and remained approximately the same in subsequent years. The low values for 1954 seem clearly the result of low rainfall; in fact, 1954 was the only year which rainfall was appreciably below normal. The difference in production between the first (1952) and the second year (1953) can not be ascribed to rainfall since it was almost exactly the same for the two years. Production was also greater during the first year in 5 out of 6 other fields in which net production was measured during the first two years after the cessation of agriculture. (See

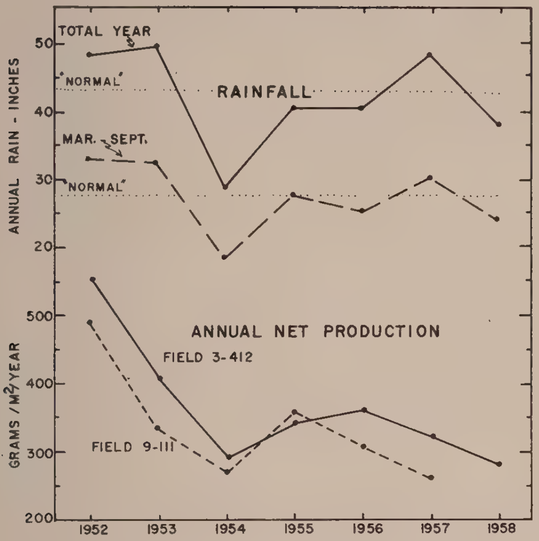

FIG. 4. Total annual net production of dry matter and rainfall during the first seven years of succession on the two intensive study fields.

Table VI for data on field 3-128). The difference was greater on light soils than on heavy soils. In the absence of any other logical explanation we attribute the high first year values to residual fertilizer remaining from the previous crop year, with phosphorus probably being the key factor. The only direct evidence for this was the fact that phosphorus (and nutrients in general) did decline in the topsoil where almost all of the roots of the annuals are located (Table III). The situation the first year resembled that of a temporary "bloom" such as often occurs in cultures where requisites have accumulated prior to the start of the culture.

To summarize, net production during the first year was generally of the order of magnitude of 500 g of dry matter per square meter per year and during subsequent years about 300 g, except when reduced by low rainfall or extreme soil type. In other words, after a one year "bloom," a steady-state in productivity was achieved even though species composition was constantly changing as was described in the previous section.

NET PRODUCTION AND SOIL

The relationship between annual net production and the silt-clay content of the subsoil is shown in Figure 5. Each point on the graph represents a different field. In order to provide a more valid comparison in which other variables are reduced, values for the "bloom" year of 1952 and the "drought" year of 1954 are not included. Therefore, the points in Figure 5 are values for the years 1953, 1955 and 1956 when, as shown in Figure 4, rainfall was essentially normal and the stage of succession had little effect on total organic production. It is evident from Figure 5 that the amount of silt and clay, which functions as water and nutrient holding material, becomes critical below 20% and especially below 15%. Above 20% the amount of silt and clay had less effect on total annual production even though (as already described) species composition was influenced to a considerable degree by high silt-clay content. Apparently, there are somewhat different species combinations in the flora which are adapted to grow at different silt-clay levels. In the intermediate range of conditions (20 to 40%) these different combinations have approximately the same ability to produce organic matter, but in the low range of silt-clay the production of the adapted community may be reduced.

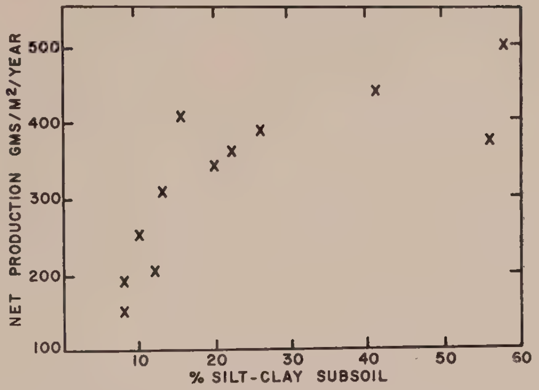

FIG. 5. Relationship between net production and the silt-clay fraction of the subsoil (A_2 or B_1 horizon). Each point on the graph represents annual production of a different field during one of the three years (1953, 1955, and 1956) when production was stabilized and rainfall was normal.

THE STANDING CROP OF LIVING AND DEAD MATERIAL

In Figure 6 seasonal and succession changes in the "standing crop" of living and dead material are shown for Field 9-111. As would be expected, the amount of living plant material was minimum in winter and maximum at the end of the growing season in late September or early October, while the amount of dead material not yet incorporated into the soil (i.e. total litter) was minimum towards the end of the growing season and maximum after the killing frosts of late October or early November. The curves for both living and dead material tended to flatten out during succession since seasonal differences in both the rate of production and rate of decomposition became

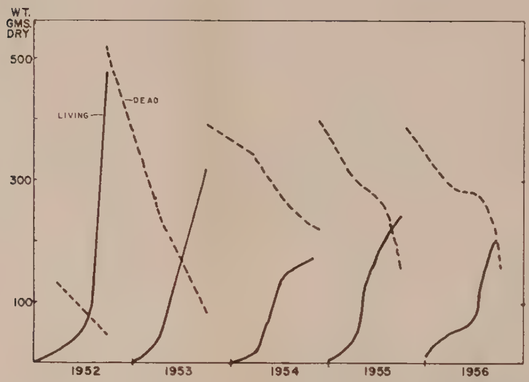

FIG. 6. Seasonal and successional changes in the standing crop of living and dead material on field 9—111 during the first five years after abandonment of agriculture. Solid line is a smoothed curve showing increase in dry matter during the growing season, while broken line is a similar curve showing decrease in dead material.

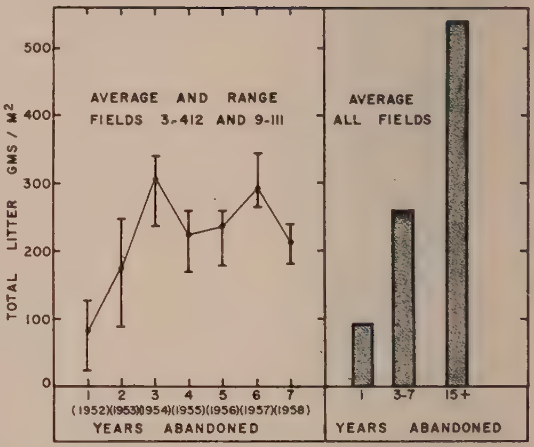

FIG. 7. Levels of litter (total dead plant material above ground) in fields of different ages. In the left hand diagram the average quantity (based on monthly samples) for the year is shown and also the lowest levels (usually occurring in September) and the highest levels (usually in November). In the bar graph on the right average levels are shown for one-year fields, 3-7 year forb fields and broomsedge fields.

less marked with the passage of time. An equilibrium between annual production and annual decomposition was essentially established after only 3 years.

Changes in total litter for both fields 9-111 and 3-412 are diagrammed in Figure 7 along with average values for all fields studied. After the harvesting of the last cultivated crops in the autumn of 1951 the small amount of litter which remained decomposed rapidly during the ensuing growing season of 1952. Since little new dead material was added until the end of the season the amount of litter reached a low point of less than 50 g of dry material per meter square in the early fall of 1952. During the next two years the amount of dead material increased and stabilized at around 250 to 350 g/m^2. It was evident that as long as annual and biennial plants remained dominant no further change in the seasonal pattern or average amount of litter would be expected. However, looking ahead to the broomsedge stage it would appear that the litter again increases and probably reaches another equilibrium as perennial grasses become dominant. As shown in Figure 7, the average amount of litter in two broomsedge fields, estimated to be at least 15 years old (the exact age was unknown since these fields had already been abandoned for a number of years at the time of the establishment of the SRP) was of the order of 500 g/m^2, or about twice the average amount present in forb fields.

Although the litter increased during the first three years of succession, the amount of organic matter in the soil itself apparently did not increase (Table III). In fact, mineralization and leaching apparently removed more organic matter from the topsoil than was replaced from decomposition of the litter during these first few years. Ultimately, however, the organic content of the soils is destined to increase since the organic content of forest soils of the region is greater than that of the abandoned fields. Whether this increase occurs during the grass stage or during the forest stages of succession remains to be seen. As Olson (1958) has shown, the buildup of organic matter in sandy soils can be a very slow process.

Since stems and leaves of some of the major species could be identified in the litter samples it was possible to follow the decomposition of the above-ground portion of an annual crop by determining the per cent remaining at successive sample periods. In Figure 8 the disappearance of the fall-maturing, first-year Leptilon, the summer-maturing Gnaphalium, and the spring annuals are shown. The large, woody stalks of the first year Leptilon decayed slowly during the winter, more rapidly during the next summer until only the thick basal portions of the stems remained in the ground litter. Segments of the basal stem 2-6 in. long were very resistant to decay and resembled miniature "logs" lying on the surface of the soil. After 6 years these segments were still recognizable in the litter as were occasional sections of corn stalks remaining from the 1951 crop. In contrast, the Gnaphalium stalks were completely decomposed within one year, and the small spring annuals were decomposed by the end of the season in which they grew. Since average size of individual plant decreased and stems became less woody after the first year, the rate of decomposition of the annual crop increased until a temporary equilibrium between production and decomposition became established.

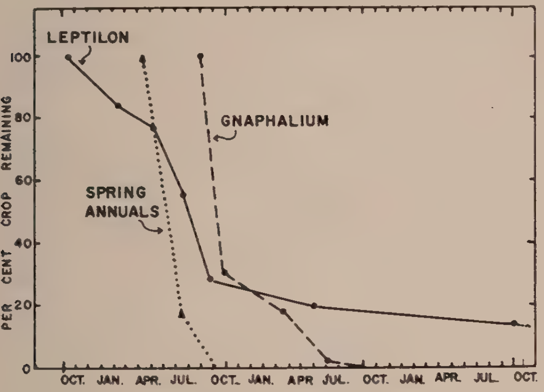

FIG. 8. Decomposition of the above-ground portions of annual crops of three types: (1) large, woody forbs as represented by first-year Leptilon, (2) summer annuals as represented by *Gnaphalium obtusifolium*, and (3) spring annuals including Rumex, Oenothera, *Gnaphalium purpureum*, Specularia and others. The per cent of the dry weight of identifiable materials in the litter at successive intervals after maturing and death of the crop is shown.

THE SEASONAL PATTERN OF NET PRODUCTION

In Table VIII and in Figure 9 net production data are given in terms of average daily rates for two-month intervals during the major growing season. As shown in Figure 8 production was low (about 1 gm./m²/day) during spring and early summer of the first year and relatively high (over 5 gms./m²/day) during the period from mid-July to mid-September. During the next several years of forb dominance, when total annual production was stabilized as previously described, the spring and early summer rates were higher but the late summer rate much lower so that the seasonal curve became much flatter (compared with the first year). Production was even more uniformly spread over the season in the two broomsedge fields studied since the spring rate was as high as or higher than that of late summer. The high spring production probably results from the fact that perennial plants were able to respond sooner than annual plants to the first favorable conditions of moisture and temperature in the spring. In fact, broomsedge often begins growth in February. It is also evident from the data that the first year "bloom" in production was the result of the high rate during the last two months of the season. Finally, as spring production increases and later summer production decreases with the progress of succession mid-summer values tend to become lower than either. High respiratory losses during the hot period may contribute to this pattern.

TABLE VIII. Seasonal and successional changes in net production rate (grams dry matter per square meter per day)

	Annual Forb Fields (Average 2 fields, 9-111 & 3-412)					Perennial Grass fields (Av. 2 fields 3-417 & 2-416)
Years abandoned.....	1	2	3	5	6	15
Year measured.......	(1952)	(1953)	(1954)	(1956)	(1957)	(1954)
Spring (March 15-May 15)..	1.0	1.4	1.1	1.2	1.6	2.2
Early Summer (May 15-July 15)........	0.7	1.6	1.8	1.4	1.4	1.5
Late Summer (July 15-Sept. 15).......	5.4	2.5	2.0	3.3	1.9	1.8
Average—6 months major growing season..........	2.7	1.8	1.6	1.8	1.6	1.9

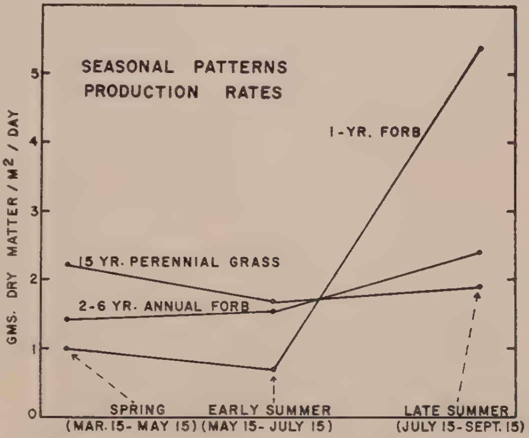

FIG. 9. Production rates for two-month intervals during the six-month major growing season for one-year fields, 2-7 year forb fields, and broomsedge fields (15+ years) illustrating the changing pattern of the seasonal distribution of production.

It is instructive to compare the old-field net production with that of other ecosystems. Comparable data on various natural and cultivated ecosystems have been recently summarized by Odum (1959: page 73, Table 7). The most fertile natural communities such as marsh grass or bottomland ragweed, as well as intensive agriculture such as sugar cane, average 10-20 g dry matter per square meter per day for periods of 6 months or more. For a 6 month growing season young forest plantations in England average 6, Nebraska tall grass prairie 3, Wyoming short grass grassland 0.5 and Nevada desert about 0.2 g/m²/day. Corn and wheat as intensively cultivated in northern Europe averages 4-8 g dry matter (including estimated straw, stubble and roots as well as the harvested grain), but the world average for both crops is 2.3. Thus, the productivity of SRP old-fields during the first year of abandonment was about the same as average corn or wheat, or natural prairie, but somewhat less than this in subsequent years (see Table VIII).

Discussion

Figure 10 summarizes the entire study and brings out certain points which seem worthy of emphasis. Six attributes which depict both the structure and the function of the community during the early stages of succession are shown. The bar graphs at the top of the Figure show the year to year changes in the relative importance of each of the six species which contributed the most to annual net production. The pattern of gradual and continuous change in species composition, as shown here, is a familiar one that has been described for other localities. The curve showing the increase in the number of species contributing at least 1 gm./m²/year to total organic production (i.e., our arbitrary definition of a "dominant") illustrates the increase in species diversity which occurred. The relationship between the terminal or maximum standing crop and the total annual production is shown in the next curve. Standing crop was an approximate measure of productivity during the first two years when production was concentrated into the last part of the season, but not in subsequent years when the standing crop at any one time was much smaller than the annual production. The rapid shift from an uneven to an even seasonal distribution of production is further shown by the curves of production rates. Finally, the stabilization of the average litter and the total annual production after about two years is shown in the bottom two curves in Figure 10.

If we consider that species composition and species diversity represent "structural" features of the community and that productivity is a "functional" attribute, then it is clear that structurally the community changed gradually and continuously but that functionally a temporary steady state was established during the period of study.

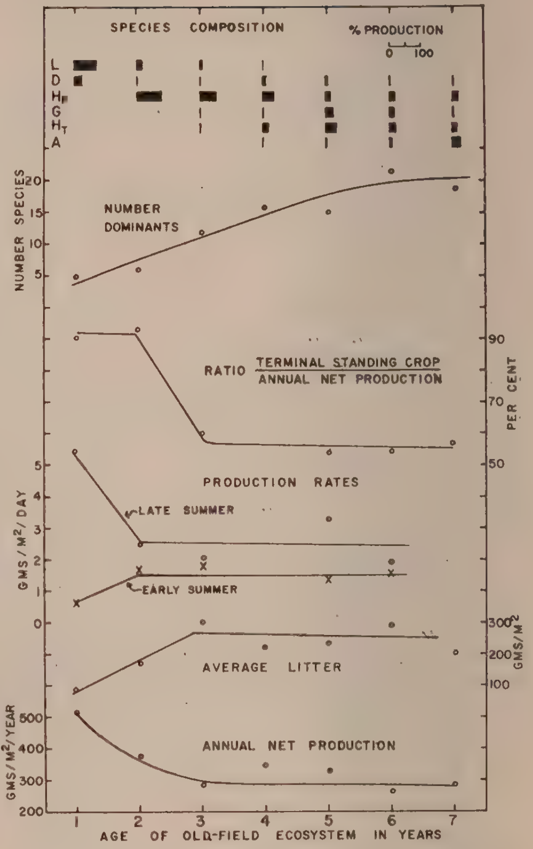

Fig. 10. Six features of the old-field ecosystem during the first seven years of natural succession comparing major structural attributes (species composition and diversity) and functional attributes (productivity). The relative importance in terms of the per cent of total annual production of six major taxa are shown in the top bar diagram. The six taxa are: L-Leptilon; D-Digitaria; H_p-Haplopappus; G-*Gnaphalium obtusifolium*; H_t-Heterotheca; A-Andropogon. The number of dominants includes all species contributing more than 1 g/m²/year to annual production. The relative stability of productivity features contrasts with marked changes in species composition and increase in species diversity.

Previous studies of secondary succession on land have emphasized the changes in species composition and the structure of the standing crop; such changes are particularly striking in the early stages of succession. Typically, dominants replace one another from year to year, the relative abundance of any one species rarely is the same from one year to the next, and the number of species and the number of individuals often increases, at least in the early years. A pattern of this sort was quite evident in the SRP fields. Because changes in the taxonomic composition of the community with time are conspicuous, gradual and continuous, it has often been inferred that productivity also must change. In fact, it has often been assumed (without actual measurements) that productivity increases automatically with succession. For example, Oosting (1956) states the generally held view that succession progresses from "fractional utilization" to "maximum utilization" and that a "peak in productivity" is reached at the climax. As is clearly shown in the present study, productivity does not necessarily change with a change in taxonomic composition, nor necessarily increase with succession. Nor does an increase in the number of species in the community necessarily increase total productivity, although increased diversity may well increase the stability of the community and its ability to adapt to changes in climate or to exploit various microenvironments in the habitat.

The reasons for the rapid change in species during the early stages of succession are not yet clear. Short life cycles, competition with later invaders and root anti-biotics are probably all involved in the succession of species. Keever (1950) has found some evidence that roots of Leptilon produce substances which inhibit the growth of second year individuals. Certainly, Leptilon, and to a lesser extent the other major forbs, decline in vigor after the first year of occupation of a site even though numerous seeds sprout.

While it is planned to continue the present study into the perennial grass and pine stages, the trends so far observed suggest a tentative hypothesis regarding the relationship of energy and succession. From the functional standpoint secondary succession seems to involve a series of temporary steady-states each associated with a major life form. For example, in so far as organic production and turnover is concerned, the years of forb dominance proved to be quite similar despite the almost complete turnover of species. It is probable that a second temporary steady-state equilibrium will be reached when broomsedge and associated perennials become fully established. Preliminary measurements indicate that the seasonal distribution of production is different, the level of organic matter higher, but the annual net production not much greater in broomsedge as compared with the forb stages. Invasion of pines will bring about other changes and another equilibrium which will tend to persist despite marked change in appearance of the community which will occur as numerous small trees give way to fewer large ones. The pine stage will likely be the final or climax stage on the lighter soils, especially if fire remains a regular part of the environment. On heavier or poorly drained soils succession may be expected to continue to a hardwood stage.

As we have seen, the forb stage on SRP fields began with a "bloom" in productivity. It seems likely that at least a temporary increase in productivity may be expected in the early stages of broomsedge and pine establishment. Such a "bloom" could result from the exploitation by the new life form of water and nutrients not available to the previous life form. Thus, the deeper roots of perennial grasses and trees probably will be able to obtain nutrients which have leached beyond the reach of the annuals. Once the accumulated requisites have been brought into the ecosystem, however, the community will adjust to the rate at which the total nutrient pool can be recycled and thus a steady-state in energy flow established. Assuming that climate and solar radiation remain the same, an established equilibrium will presumably persist until additional limiting materials are either brought into or lost from the system.

SUMMARY

Energy flow through communities which develop on abandoned farmland is being studied on the AEC Savannah River Plant reservation. The present report is concerned with net primary production during the first seven years of secondary succession.

Net production was measured by what may be termed the "short-term harvest method" which involved harvesting at monthly intervals all organic materials from meter quadrats along a transect. Since heterotrophic utilization was mostly delayed in time during the early stages of succession the measured "net community production" approximates true net primary production.

The general pattern of succession was observed on 600 reference fields, productivity and soil measurements were made on 30 selected study fields representing the eight major agricultural soil series, and intensive studies were carried out on two of the study fields which represented two of the major soils and the two physiographic subregions of the SRP reservation.

Annual and biennial forbs produced most of the organic matter during the first five years with *Leptilon canadense, Haplopappus divaricatus,* and *Heterotheca subaxillaris* appearing as major dominants in that order on well-drained soils. The perennial grass, Andropogon ("broomsedge"), did not begin to contribute appreciably to production until the 5th to 7th year.

The vegetation was similar in general appearance on most soil types during the first year, but species composition showed increasing divergence on different soils in subsequent years. The silt-clay content of the subsoil (A_2 or B_1 horizons) was a key factor influencing species composition, the number of dominants (arbitrarily designated as species producing more than 1 gm. dry matter/m^2/year), and the rate of succession of species. In general, species composition changed more

rapidly, broomsedge (Andropogon) and pines invaded more rapidly, and the number of dominants was greater on the heavier soils as compared with the light, sandy ones.

Organic matter and major mineral nutrients did not increase in the soil during the first three years; in fact, these materials decreased in the topsoil on sandy soils indicating that leaching exceeded the rate of decomposition and nutrient regeneration in the topsoil.

Net production during the first year was of the order of 500 grams of dry matter per square meter per year, and during subsequent years about 300 grams, except where reduced by low rainfall or extreme soil type. In other words, after a one year "bloom" (tentatively attributed to residual fertilizer or other requisites remaining from agricultural use), a steady-state in productivity was achieved even though species composition was changing from year to year.

Annual net production (in contrast to species composition) was not greatly different on different soil types as long as the water and nutrient holding silt-clay fraction was greater than 20%; below 15% there was a marked reduction in productivity.

A temporary equilibrium between annual net production and annual decomposition of dead plant material was established after three years when the average litter became stabilized at around 250-350 grams of dry matter per square meter. Preliminary measurements of fields already abandoned at the time of establishment of SRP indicated that the "standing crop" of dead matter may be expected to increase with the invasion of perennial grasses.

The seasonal pattern of production changed with succession. Production rate was low (about 1 $g/m^2/day$) during spring and summer of the first year and relatively high (about 5 $g/m^2/day$) during the period from mid-July to mid-September. During the subsequent years of forb dominance, when annual production became stabilized, spring and summer rates were higher but late summer rates much lower so that the seasonal curve became much flatter, and maximum or terminal standing crops became smaller.

The average production rate of 1-3 $g/m^2/day$ of SRP old-fields during the 6 month major growing season is about the same as world average wheat or corn, or natural prairie computed for the same time period.

If we consider that species composition and species diversity represent "structural" features of the community and that productivity is a "functional" attribute, then it is clear that structurally the "old-field" commmunity changed gradually and continuously, but that functionally a temporary steady-state was established during the period of forb dominance. The study clearly showed that productivity does not necessarily change with a change in species, nor necessarily increase with succession as has often been assumed.

The trends so far observed suggest a tentative hypothesis regarding the relationship of energy to succession. From the functional standpoint succession may involve a series of steady-states each associated with a major life form rather than a continuous change associated with species change as is usually postulated. It may be further suggested that an increase in productivity, even if only a temporary "bloom," would be most likely to occur in transition from one life form to another since a new life form may be able to utilize accumulated limiting materials not available to the previous life form.

APPENDIX: CHECKLIST OF MAJOR SRP OLD-FIELD DOMINANTS

Forbs (Dicots)

Rumex Acetosella L.	Sheep-sorrell
Lepidium virginicum L.	Pepper "grass"
Rubus hispidus L.	Southern dewberry
Cassia (Chamaecrista) fasciculata Michx.	Partridge-pea
Lespedeza striata (Thunb)	Annual Lespedeza
Hypericum gentianoides L.	Pineweed
Lechea villosa Ell.	Pineweed
Oenothera laciniata Hill	Evening-primrose
Polypremum procumbens L.	—
Linaria canadensis (L.)	Blue Toadflax
Bignonia radicans L.	Trumpet-creeper
Diodia teres Walt	Buttonweed
Specularia perfoliata (L.)	Venus's Looking-glass
Ambrosia artemisiifolia L.	Ragweed
Eupatorium capillifolium (Lam.)	Dog-fennel
Eupatorium compositifolium Walt	Dog-fennel
Heterotheca subaxillaris (Lam.)	Camphorweed
Haplopappus (Isopappus) divaricatus (Nutt.)	Yellow Aster
Erigeron annuus (L.)	Daisy-fleabane
Leptilon (Erigeron) canadensis (L.) Britton	Horseweed
Gnaphalium obtusifolium L.	Rabbit-tobacco
Gnaphalium purpureum L.	Purple Cudweed
Grasses and Sedges	(Monocots)
Festuca sciurea Nutt.	Fescue-grass
Eragrostis spectabilis (Pursh)	Tumble-grass

Triplasis purpurea (Walt)	Sand-grass
Aristida tuberculosa Nutt.	Three-awn Grass
Aristida purpurascens Pois	Arrowfeather
Cynodon dactylon (L.)	Bermuda Grass
Digitaria sanguinalis (L.)	Crab-grass
Leptoloma cognatum (Schultes)	Fall Witchgrass
Panicum virgatum L.	Switchgrass
Cenchrus pauciflorus Benth.	Field Sand-spur
Andropogon virginicus L.	Broom-sedge
Andropogon ternarius Michx.	Broom-sedge
Sorghum halepense Pers.	Johnson-grass
Cyperus rotundus L.	Nut-grass

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THE EFFECTS OF BURNING ON THE MULCH STRUCTURE AND SPECIES COMPOSITION OF GRASSLANDS IN WESTERN NORTH DAKOTA[1]

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The universal coincidence of grassland vegetation and frequent fire has led to considerable speculation on the nature of their interrelationships (Sauer 1950; Stewart 1951, 1956). The historic occurrence of the relationship is clear; the compilation of a catalog of presettlement and settlement references to fire within any geographical grassland region would appear possible, as has been done for the Midwest by Stout (1944) and for the Desert Grassland by Humphrey (1958). Theodore Roosevelt (1885), to take but one example from the settlement period of western North Dakota, has left a vivid description of prairie fire: "From a hill we looked back through the pitchy night at the fire we had failed to conquer. . . . In the darkness it looked like the rush of a mighty army, bearing triumphantly onward, ... Fire is one of the most dreaded enemies of the ranchman on the cattle ranges; and fighting a big prairie fire is a work of extraordinary labor, and sometimes of danger." Grassland fires, though now greatly reduced in the area burned, are still common in western North Dakota, and apparently have been so from antiquity.

A long-term study on the phytosociology of grasslands in western North Dakota was recently initiated and the importance of evaluating fire as an ecological factor has become evident. It is the purpose of the present paper to report the results of a preliminary quantitative study of the mulch structure and species composition on three natural grasslands following fires of known age. The paucity of quantitative data on the fire-grassland relationships in the Northern Plains would appear to justify the presentation of these initial studies. It is hoped that a more comprehensive report on the relationship will be possible after the burns reported here have been followed for a number of years and after additional burns, occurring under a variety of environmental conditions (e.g., soil types, weather conditions, exposures, slopes, etc.) have been found and followed.

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METHODS

The design of the study was to use pairs of stand in which the partners of each pair were as identical as possible with the exception that one member of each pair had been burned and the other member had not been burned. In this way, the burned stand served as the "treatment area" and the unburned stand served as the "control area." Three pairs of stands were chosen for study and these areas are described in detail below. The species composition of each stand was determined by the frequency method; each stand was sampled by employing forty ¼ m² quadrats which were distributed at evenly spaced distances throughout the stand. Quadrats of this size and number had been previously shown to give an adequate sample of vegetation (Dix 1958). The natural mulches were clipped and segregated according to methods described by Dyksterhuis and Schmutz (1947). Under this system, the cover of natural grassland is segregated into three classes: (1) *Herbage* consists of the plant material produced during the current growing season; (2) *Fresh Mulch* is the residuum of the past few growing seasons which has remained bulky and, though weathered, largely undecomposed; and (3) *Humic Mulch* consists of the relatively dense, partially decayed, disintegrated and fragmented organic residuum which lies on and directly above the mineral soil. In the present study five ¼ m² quadrats were clipped in each stand, the various cover types segregated, and their air-dry weights determined. These data are given in air-dry weights to make them more directly comparable with existing literature. The clipped mulches were also oven-dried and a good correlation was found between air-dry and oven-dry weights. Oven-dry weights of this material may be closely approximated by subtracting 5% of their air-dry weight.

The exposures of the stands were determined with a hand compass and their slopes were measured with an Abney level. These exposures have been corrected for magnetic declination.

The field work for the study was done between August 14-18, 1958. At this time the vegetation had completed its growth for the year and was in the process of curing. The figures in Table III represent the maximum production for the year.

The taxonomic nomenclature is according to Stevens (1950).

STUDY AREAS

All of the stands sampled in the present study occur in Billings and McKenzie Counties in Western North Dakota. This "badlands" area has been formed by the rapid downcutting of the Little Missouri River through the stratified and largely unconsolidated Paleocene materials of the Fort Union Group, Tongue River formation (Leonard 1930). The climate is the continental, semiarid type with short warm summers and long cold winters. The frost-free season averages about 111 days. The mean annual precipitation is approximately 16 in., about one-half of which occurs in the spring and early summer months. The soils of the area, due to the "badlands" topography and the heterogeneity of parent materials, are highly variable and have been classified by Edwards and Albeiter (1942, 1944). The native vegetation consists principally of grassland, although woody vegetation usually occupies draws and creek and river bottomlands. These grasslands are diverse; the flat upland sites usually support *Stipa comata, Bouteloua gracilis* and *Carex filifolia,* to which are added *Calamovilfa longifolia* on sandy soils and *Agropyron smithii* on clay soils. On steep northern slopes (15° or more) *Andropogon scoparius, Muhlenbergia cuspidata* and *Agropyron dasystachum* are usually the dominant species. The vegetation of this area has been discussed by Hanson and Whitman (1938), Quinnild and Cosby (1958), Dix (1958), and others.

All of the stands occur within the borders of Theodore Roosevelt National Memorial Park. The South Unit of this Park was fenced in the summer of 1956, and the fencing of the North Unit is scheduled for completion in the summer of 1959. Both units have been under the jurisdiction of various state and federal agencies since the early 1930's and, during that time, grazing has been limited to trespassing cattle and horses of unknown numbers. The fire atlas of the Park has been continuously maintained since the 1930's, and it seems reasonable to assume that areas not recorded as having been burned in the atlas have been fire free for at least 20 years.

The names applied to the stands of this study are the designations used in the fire atlas of the Park.

Dedication Hill

These stands are located within the borders of the South Unit of the Park at SW¼ sec. 27, T. 140 N. R. 101 W. This upland site appears to have been grazed only lightly in the past and has been ungrazed since 1956. The stands occur on Flasher loamy fine sands, have exposures of 15° west of north and slopes of 10°. The fire on the burned stand occurred on August 14, 1954 and covered an area of 3.2 acres. The partner stands are approximately one-quarter mile apart. No erosion was apparent in these stands.

Squaw Creek

These stands are located on a creek flat with no measurable slope at NW¼ sec. 30, T. 148 N. R. 99 W. in the North Unit of the Park. Trespass cattle are frequently seen in this area although in no case could grazing pressure be considered to be more than moderate. The soils are classified as belonging to the undifferentiated alluvial clay loam type. This fire occurred on September 30, 1955 and covered an area of 110 acres. The fire-free partner of this stand is located approximately 200 yards south and across a small draw from the burned stand. Measurement with an Abney level showed the partner stands to be at the same elevation. No soil erosion was observable in the stands.

North Rim

Located at SE¼ sec. 29, T. 148 N. R. 99W. in the North Unit of the Park, these upland stands have exposures 25° south of west and slopes of 10°. They occur on Flasher fine sandy loam and were judged to be lightly grazed by trespassing livestock. The burn occurred on May 29, 1958 and covered 2.5 acres. The fire-free partner is immediately adjacent to and north of the burn. No soil erosion was present in the stands.

RESULTS

The species compositions of the six stands are presented in Table I. An examination of this table shows the frequency values of most species to be relatively similar in the burned and unburned stand partners. Notable exceptions for several species occur, however, in the Dedication Hill stands. *Artemisia glauca* has a strikingly higher frequency in the burned than in the unburned stand, while *Lactuca pulchella, Calamovilfa longifolia* and *Selaginella densa* have higher frequencies in the unburned stand. Observations in the general area of the study indicate that *Artemisia glauca* tends to be rather weedy in its habitat tolerances and is often found along roadsides and in disturbed sandy soils. The reduction in competition in the stand following fire, perhaps due to the reduction in vigor of other species, may account for this increase in frequency. *Lactuca pulchella,* like *Artemisia glauca,* appears to be rather weedy in its habitat tolerances, and its behavior here is puzzling. No explanation can be offered at this time for the lower frequencies of *Lactuca pulchella, Calamovilfa longifolia* and *Selaginella densa* in the burned stand on Dedication Hill. However, the similarities in frequency values for these same species in the burned and unburned North Rim stands (Table I) are not necessarily opposed to the view that the differences noted between the Dedication Hill stands are significant, since a marked change in the frequency index values of perennial herbs would not be expected to occur during the first growing season following fire. Any interpretation placed on these differences must be viewed as no more than suggestive, due to the limited nature of the study.

TABLE I. Frequency index values for the leading species of the study. Only those species with frequency index values of at least 15% in at least one stand are listed.

	DEDICATION HILL		SQUAW CREEK		NORTH RIM	
	Unburned	Burned	Unburned	Burned	Unburned	Burned
Graminoids						
Agropyron dasystachum	10	27	0	0	20	15
Agropyron smithii	0	7	100	90	60	67
Bouteloua gracilis	62	60	92	97	80	72
Carex eleocharis	12	5	27	27	32	55
Carex filifolia	95	92	17	2	82	85
Carex pennsylvanica	37	5	5	5	15	25
Calamovilfa longifolia	70	22	0	0	25	17
Koeleria cristata	55	75	0	0	30	35
Muhlenbergia cuspidata	2	0	0	0	55	50
Stipa comata	92	90	42	52	67	47
Stipa viridula	0	0	5	0	30	17
Forbs						
Artemisia glauca	30	82	0	0	22	22
Artemisia frigida	15	25	17	7	42	10
Aster oblongifolius	5	0	0	2	32	27
Brauneria angustifolia	2	0	0	0	32	40
Chrysopsis villosa	22	0	0	0	0	0
Euphorbia esula	0	0	17	0	0	0
Gaura coccinea	5	0	0	0	22	17
Hemeoma hispida	2	0	20	40	7	0
Lactucca pulchella	75	12	0	2	27	25
Lappula redowski	0	0	2	17	0	7
Liatris punctata	5	5	0	0	25	17
Lithospermum incisum	15	2	0	0	2	0
Lygodesmia juncea	30	22	0	2	7	2
Petalostemum purpureum	25	2	0	0	7	10
Psoralea argophylla	15	10	0	0	10	2
Rosa arkansas	12	5	0	0	17	7
Selaginella densa	80	7	15	2	2	0
Sphaeralcea coccinea	0	0	12	42	10	12
Total Number of Species	51	31	19	26	49	38
Sum of Stand Frequencies	875	600	407	458	872	740

In order to evaluate differences in the overall species composition of the stand pairs, an index of similarity was employed:

$$K = \frac{2w}{a + b} \times 100$$

In this formula K is the coefficient of similarity between two stands (A and B), a is the sum of frequencies for all species in stand A, b is the sum of frequencies for all species in stand B, and w is the sum of frequencies shared by those species which occur in both stands. Thus, when stands are identical in species composition, K = 100 (i.e., the stands are 100% alike) and when two stands have no species in common, K = 0.

The similarity coefficients for all six stands of the study are presented in Table II. It is evident from this table that the similarity values were greatest between the partner stands. These similarities are interpreted to indicate that, although a few individual species may have been strongly influenced, a single fire did not greatly alter the overall species composition of these stands. It is perhaps significant, however, that differences in species composition between the burned-unburned stands in the four-year-old burn on Dedication Hill were greater than were differences in species composition between the stands in the one-year-old burn on the North Rim. This lag in compositional adjustment can probably be accounted for by the virtually complete survival of perennial plants observed on the burned North Rim stand three months after the fire. With almost complete survival, the frequency index values of the perennial plants did not change greatly during the first year. In time, however, fire-induced changes in the environment are likely to be reflected in compositional adjustments within the community, as suggested in the frequency differences between the Dedication Hill stands.

TABLE II. Indices of stand similarity. The numbers are in percent. The numbers in bold face type indicate comparisons between partner stands

		DEDICATION HILL		SQUAW CREEK		NORTH RIM	
		Unburned	Burned	Unburned	Burned	Unburned	Burned
Dedication Hill	Unburned. .	. .	**67**	35	23	50	49
	Burned.	. .	. .	32	28	53	51
Squaw Creek	Unburned. .	. .	. .	. .	**83**	44	45
	Burned.	. .	. .	. .	. .	41	42
North Rim	Unburned. .	. .	. .	. .	. .	. .	**73**
	Burned. . . .	.					

Table II also shows that the Dedication Hill and North Rim stands are more closely related to each other than to the Squaw Creek stands. This would be expected from an examination of their soils; the Dedication Hill and North Rim stands occur on a sandy loam while the Squaw Creek stands occur on a clay loam soil.

The results of the clipping studies are presented in Table III. The most striking results of these studies are the remarkable similarities between complementary herbage and mulch classes for the two partner stands on Dedication Hill. These results indicate that following fire only four growing seasons were required to rebuild the mulch structure of this grassland type. The Squaw Creek burned stand also appeared to be making a rapid recovery following fire and this stand may be expected to have rebuilt its mulch structure at the end of two or three additional growing seasons. The North Rim stands show that the production of herbage during the 1958 growing season was significantly less in the burned as compared to the unburned stand. The lateness of the North Rim fire (May 29) probably retarded the year's herbage production in addition to removing all top growth that had been made prior to burning. The complete destruction of the fresh mulch in this stand attests to the severity of the fire. The 579 lbs/acre of humic mulch found on the North Rim burned stand were undoubtedly the remains of the humic mulch present at the time of the fire. This is of interest since it shows that approximately 12% of the humic mulch survived the fire. This residue was unquestionably of great importance in preventing water and wind erosion and in maintaining a favorable rate of water infiltration during the period between the burn and the maturation of the first season's herbage.

TABLE III. Effects of fire on three grassland stands in western North Dakota as reflected in pounds per acre of air-dry herbage and natural mulches. All stands were clipped in mid-August, 1958. Vegetal cover protected from fire for many years is contrasted with cover on adjacent recently burned areas. Burned-unburned partner stands were selected to be otherwise comparable, considering slope, exposure, soil and vegetation type. The date on which each stand was burned is given in the column heading

	DEDICATION HILL		SQUAW CREEK		NORTH RIM	
	Unburned	Burned Aug. 14, 1954	Unburned	Burned Sept. 30, 1955	Unburned	Burned May 2 , 1958
Herbage.	1,995	1,599	1,708	1,700	1,712	906
Fresh Mulch. . .	1,185	1,214	1,647	756	1,829	0
Humic Mulch. .	3,355	3,784	4,229	2,784	4,860	579
Totals.	6,535	6,597	7,584	5,240	8,401	1,485

Although no quantitative data were taken on the effects of burning on flower production, it is perhaps worth recording that *Stipa comata, S. viridula,* and *Agropyron smithii* were not found in flower on the burned North Rim stand, while conversely, *Bouteloua curtipendula, Andropogon scoparius, Calamovilfa longifolia,* and *Brauneria angustifolia* were commonly found in flower. Flowering individuals of all these species were frequently found on the unburned partner. The stimulation of flower production by fire has been reported by Curtis and Partch (1950) and Dix and Butler (1954) for Midwestern grassland and by Burton (1944) for several Southern grasses. However, no reference to the effects of fire on flower production in the Northern Plains grassland has come to the attention of the author.

Discussion

The characteristics and influences of natural mulches on grasslands have received widespread attention during recent years (Dyksterhuis and Schmutz 1947; Weaver and Rowland 1952; Hopkins 1954; Heady 1956; Quinnild and Cosby 1958; and others). The work of Quinnild and Cosby on two isolated relict mesas in western North Dakota is particularly pertinent to the present study, since both investigations were carried out in the same general area and since the methods of herbage and mulch sampling are directly comparable. When the dominance of *Stipa comata* was used as a criterion for comparison, good agreement was found between the total herbage and mulch weights for the unburned Dedication Hill and North Rim stands and the *Stipa comata-Koelaria cristata* community of the relict mesas, with 6,500, 8,400 and 7,300 pounds per acre, respectively. In Stipa stands of the present study, however, the fresh mulch weights were less and the humic mulch weights more than the weights for the comparable mulch classes on the relict mesas. These differences were perhaps due to the recent history of grazing on the stands of the present study. The trampling effect of livestock brought much of the fresh mulch material into direct contact with the soil surface and thereby accelerated its conversion into humic mulch. A similar occurrence was reported by Dyksterhuis and Schmutz (1947) on the Fort Worth Prairie; they found the fresh mulch weight to be greatest on relict climax priarie while humic mulch had its greatest weight on range land in excellent condition.

Comparisons between the unburned Squaw Creek stand and the *Agropyron smithii* community of Quinnild and Cosby demonstrate that, although the herbage weights were rather similar (1,700 lbs./acre for Squaw Creek and 2,200 lbs./acre for the relict mesas), the fresh and humic mulch weights showed marked differences. (The herbage and mulch weights listed above and below for the *Agropyron smithii* community of the relict mesas are averages of two stands). On the unburned Squaw Creek stand, the weights for fresh and humic mulch were 1,650 and 4,200 lbs/acre, respectively, while on the relict mesas, the fresh mulch averaged 5,000 and the humic mulch 9,000 lbs/acre. The Squaw Creek stands were the most heavily grazed of the study (see Study Areas) and the most likely explanation for these differences appears to be livestock grazing and the accompanying trampling. Thus, when all the unburned stands of the present study and the relict stands of Quinnild and Cosby are considered together, it appears that light grazing tends to increase the weight of humic mulch at the expense of fresh mulch, while moderate grazing, with the accompanying compaction of the mulch and the subsequent increase in microbial decomposition (McCalla 1943), tends to decrease both the fresh and humic mulch complements.

The production of herbage on the stands of the present study and on the Stipa-Koeleria and *Agropyron smithii* communities of Quinnild and Cosby was remarkably similar. The burned North Rim stand must be excluded from this comparison because of its late spring burning, which unquestionably destroyed a part of the current year's herbage production. These similarities are interpreted to indicate that the accumulation of the fresh and humic mulches on these areas did not retard herbage production. For example, slightly more herbage was produced on the *Agropyron smithii* stands of the relict mesas, with 5,000 lbs of fresh and 9,000 lbs of humic mulch per acre, than on the burned Squaw Creek stand, with only 750 lbs of fresh and 2,800 lbs of humic mulch per acre. Similarly, herbage production was positively correlated with mulch accumulation on unburned and completely protected relict grassland in southwestern South Dakota (Larson and Whitman 1942). These results, however, are in contrast with reports of the retardation of plant heights (Curtis and Partch 1950) and forage production (Weaver and Rowland 1952) by mulch accumulation on the tall-grass prairies of the Midwest. The lower stature of the vegetation in the Northern Plains, and consequently a lower percentage of light interception, is suggested as a possible explanation for this discrepancy.

Although grassland mulches have been the recipients of considerable recent attention, their rates of accumulation have not been previously reported. It is apparent from the Dedication Hill stands that the mulch structure of the burned partner had completely recovered by the end of the fourth growing season following the burn. The burned stand on Squaw Creek, as indicated by the weights of fresh and humic mulches, appears to be recovering at a slightly slower rate than did the Dedication Hill stand. However, two additional growing seasons would appear sufficient time for this weight to return to its pre-fire condition, as judged by the unburned Squaw Creek stand. Two factors appear to be largely responsible for this slower recovery rate: (1) the heavier grazing pressure on the Squaw Creek stand; and (2) the differences in species composition. Clarke, Tisdale and Skorglund (1943), working in the grasslands of southwestern Saskatchewan, reported that the recovery of herbage production following fire was significantly retarded by grazing, and that reductions in yields following burning were greater on vegetation of the "Agropyron type" than on communities dominated by *Bouteloua gracilis* and *Stipa comata*. A comparison of Table I with the Saskatchewan stands showed the Squaw Creek stands to be similar in species composition to the "Agropyron type" of these authors. Similarly, the Dedication Hill stands appeared closely related to their Bouteloua-Stipa community.

The relict mesas investigated by Quinnild and Cosby (1958) were reported to have been fire free for at least 16 years and to be completely free from grazing, although one mesa had been mowed during the mid 1930's. The authors state that the mulch weights on these relict grasslands ". . . must reflect the approximate poundage to which it accumulates in reaching dynamic equilibrium between annual additions from growth of previous years and mineralization through decay." The Dedication Hill stands and the unburned North Rim stand appear to have closely approximated this equilibrium, with total mulch weights of 85%, 94% and 113%, respectively, of the Stipa-Koeleria relict stand. The unburned Squaw Creek stand, however, had a total mulch weight of only 42% of that found on the relict *Agropyron smithii* community. It appears likely, therefore, that the weights for fresh and humic mulch in the unburned Squaw Creek stand would increase with protection from grazing.

The production of herbage on the stands of the present study showed no evidences of retardation beyond the second year following burning. This is in agreement with the reports of Clarke, Tisdale and Skorglund (1943) in which it was found that, following fire, herbage production was reduced by 30-50% the first year, 0-15% the second year and in the following year no significant reduction could be detected. They found that fall burning, as contrasted with spring burning, caused a smaller decrease in herbage production.

On the burned Dedication Hill stand, the 1,600 lbs/acre of herbage produced during the 1958 growing season was approximately one-third of the sum of the fresh and humic mulch complements. Since this fire occurred in August of 1954, most of the organic materials in the fresh and humic classes in 1958 must have been produced during the 1955, 1956 and 1957 growing seasons. The structure of the grassland cover at the end of the 1955 growing season was probably composed of 1,100 lbs of herbage, no fresh mulch, and 400 lbs of humic mulch per acre. These figures were obtained by subtracting 30% of the 1958 herbage weight to simulate the decrease in forage production reported by Clarke, Tisdale and Skorglund (1943) for fall burning; the zero figure for the fresh mulch class was suggested by the burned North Rim stand; and the 400 lbs of humic mulch was suggested by the 12% residue mulch found on the North Rim stand after the fire and calculated by taking 12% of the humic mulch found on the unburned Dedication Hill stand. When the estimated total herbage production for 1955, 1956 and 1957 was added (assuming 1,100, 1,600 and 1,600 lbs/acre for these years, respectively) a sum of 4,300 lbs was obtained, and this sum was only 86% of the total fresh and humic mulch actually found on the ground. Two tenable explanations are suggested to account for this apparent incongruity. First, more herbage may have been produced during the 1955, 1956 and 1957 growing seasons than was estimated from the clipped weights taken in 1958. The 1957 growing season, for example, was particularly favorable for plant growth. Secondly, more humic mulch may have remained after the burn than the estimated 400 lbs. The second of these suggestions seems more credible, since 430 lbs/acre more humic mulch was found on the burned Dedication Hill stand than on its unburned partner in 1958. It is very possible, however, that both greater production in other years and a greater residue of humic mulch following burning contributed to the high humic and fresh mulch complements in this stand.

It appears from the above that virtually no decomposition of plant material occurred on the burned Dedication Hill stand from the time of the fire to the time of sampling. These results are consistent with reports on previous studies. Hopkins (1954), working in western Kansas, found that three or four years were required for the decomposition of natural grassland herbage and McCalla (1943), also in Kansas, has shown that very little decomposition occurs until the organic materials come into close contact with the mineral soil. The rate of organic decomposition appears related to the degree of compaction and depth, and hence evaporative potential of the mulch mat: as the mulch mat increases, water loss from organic materials is retarded and conditions are made more favorable for microbial decomposition. Thus, following fire, the rate of organic decomposition appears to be remarkably slow for several years. As the degree of compaction and depth of the organic mat increase, however, the rate of decomposition also increases until an equilibrium between the annual herbage production and annual decomposition becomes established. On the Dedication Hill stand this time appeared to be four years.

The results of this investigation suggest that the surficial organic matter of grasslands responds to treatments in characteristic ways, and that further study of the behavior patterns of the various herbage and mulch classes under various treatments, natural or man imposed, offers a promising approach to a better understanding of grassland vegetation. If such studies are to have maximum comparative value, however, there is an evident need for the standardization of terminology and sampling procedure. In the present study, for example, comparisons between the herbage and mulch compositions in our stands and stands reported in the literature were made difficult, and sometimes impossible, by apparent differences in terminology and sampling procedure. The classification system for the surficial organic matter of grasslands proposed by Dyksterhuis and Schmutz (1947) was found in the present investigation to be readily applicable in the field. It is suggested, therefore, that the general application of this system would greatly expedite our understanding of the role of mulches in the grassland community, much as the standardization of the terminology applied to soil horizons has aided our appreciation of the dynamics of the soil profile.

SUMMARY

This paper reports the results of a preliminary quantitative study of the species composition, herbage production and mulch structure on natural grasslands following fire of known age in western North Dakota. Partner pairs of stands, one burned and the other unburned, were sampled. In three pairs of such stands, the species composition was determined by employing 40 $\frac{1}{4}$ m^2 quadrats in each stand and the surficial organic matter was clipped and segregated according to the system described by Dyksterhuis and Schmutz (1947).

The results of the study showed the frequency values of most species to be relatively similar on the burned-unburned partner stands. Notable exceptions occurred in one stand, however, for *Artemisia glauca,* which had a higher frequency in the burned than in the unburned stand. *Lactuca pulchella, Calamovilfa longifolia* and *Selaginella densa* had higher frequencies in the unburned partner. No suggestion was offered to explain these behaviors, except in the case of *Artemisia glauca* where the general weedy habit of the species appeared to account for its increase following fire. The greatest differences in species composition were found on the oldest burn, suggesting a lag in the adjustment of perennial species to the fire modified environment.

In order to evaluate differences in overall species composition of the stands, an index of stand similarity was employed. This analysis showed the similarities between partner stands to be consistently greater than similarities between any stands other than partners.

The results of the clipping studies showed a remarkably rapid recovery of the mulch structure on a *Stipa comata* stand which had been burned in 1954. The mulch structure had completely recovered by the end of the fourth growing season following the burn. The mulch structure on a burned *Agropyron smithii* stand also appeared to be making a rapid recovery, although at a somewhat slower rate than in the Stipa stand. This difference appeared to be due to heavier and more recent grazing on the Agropyron stand and also to an inherent slower recovery rate of the Agropyron community.

Detailed comparisons were made between the results of the present study and the results reported from a previous study on two isolated mesas in Wetern North Dakota. These comparisons indicated that: (1) the annual production of herbage on the *Stipa comata* community was approximately 1,900 lbs of air-dried material per acre; (2) the average total mulch on the Stipa community was approximately 5,500 lbs/acre; (3) the accumulation of fresh and humic mulches did not retard the production of herbage in either the Stipa or Agropyron communities; (4) light grazing tended to increase the amount of humic mulch and decrease the amount of fresh mulch on a stand; (5) moderate grazing tended to de-

crease both the fresh and humic mulch weights on a stand.

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TRANSFER OF DYE THROUGH NATURAL ROOT GRAFTS OF *PINUS STROBUS* L.

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Introduction

Natural intraspecific root grafting is common in most, if not all, forest tree species. It has recently been pointed out (Bormann and Graham 1959) that, in pure stands of eastern white pine, *Pinus strobus* L., the grafting begins at an early age and leads to mature stands consisting of much-grafted unions of from 2 to many trees interspersed with occasional ungrafted individuals. The physiological mechanisms which come into play during the maturation of such a stand must be many and varied, and their ecological implications are far-reaching.

In two research areas of practical importance the role of natural root grafting is being currently brought into sharper focus. The interest of plant pathologists has been renewed by the relatively recent discovery that root grafts can transmit the organisms of Dutch elm disease, *Ceratostomella ulmi* (Schwarz) Buisman, and oak wilt, *Endoconidiophora fagacearum* Bretz, although grafts have been sporadically reported as transmission paths for pathogenic organisms for more than half a century.

In the area of forest management, the number of reports of so-called "backflash," incident to the use of silvicides, is growing. Backflash is the movement of poison, through root grafts, from

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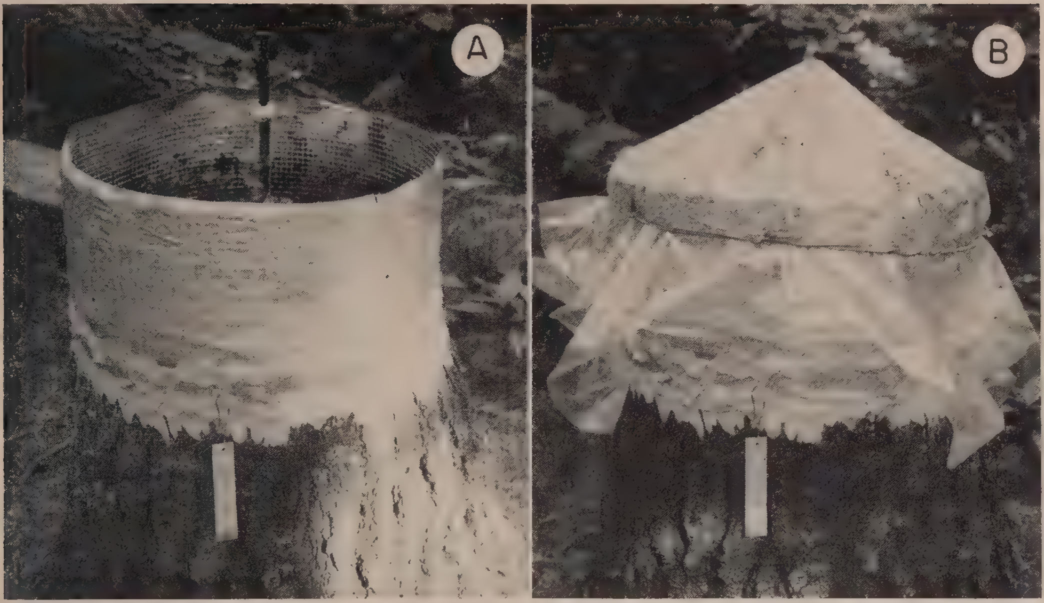

FIG. 1. Collar for retaining dye on the cut surface of a donor stump. A) Collar open, showing hardware-cloth inner cylinder and central spike with attached ruler for reading changes in dye-level. B) Polyethylene cover in place. (The tag is 9.0 cm long.)

poisoned trees to unpoisoned trees. The resulting damage may be inconspicuous and negligible, or it may be very serious, killing large numbers of desirable trees (Bormann and Graham 1960). In the matter of poison transfer, and in many instances of pathogen transmission, the process of translocation of solutions or spore is involved. Although some workers have studied the mechanisms of translocation incident to intraspecific root grafts (Neeff 1922, Yli-Vakkuri 1953, Kuntz and Riker 1956), much of the physiology of these organic root unions remains to be understood.

In the summer of 1957, as a part of a study of root grafting in eastern white pine, certain characteristics of the movement of dye into freshly cut pine stumps, thought to be heavily grafted, were observed. Preliminary tests of injection techniques, and observations of intake and transfer of solutions by the stumps of felled trees, had suggested the following questions, answers to which were the objective of the work here reported: What is the normal rate of movement of dye into grafted white pine stumps? Is the rate at which dye is taken in through grafted pine stumps influenced by weather conditions? Is there any periodicity or diurnal fluctuation in the rate of dye intake by grafted stumps?

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METHODS

Ten circular experimental plots were established in a portion of the Dartmouth Forest south of Balch Hill Road, in Hanover, New Hampshire. Each plot had a 6.1 m radius with, at its center, the stump of a freshly cut vigorous tree, the "donor." The donor trees were from 30 to 70 years old, and from 18 to 48 cm d.b.h. Other trees on the plots, if found to be grafted to a donor, were referred to as "receptors." Plots were dispersed enough to minimize the chance that dye might move from one plot to another.

About the top of each donor stump a stout watertight collar (Fig. 1a) was constructed as described by Bormann and Graham (1959). A long spike, driven into the center of the stump-top so as to project above the top of the collar, held a vertical ruler from which changes in dye-level were read. The spike also supported a polyethylene cover which prevented evaporation and excluded precipitation and falling litter (Fig. 1b). A dye tracer, 0.15% aqueous acid fuchsin, was poured into each collar to a depth of 5 cm. For 36 hours following injection, bihourly readings of dye intake were recorded. At each reading the dye depth was restored to 5 cm. After 36 hours, and for 8 additional days, readings were made at 8 am and 8 pm. During the 10-day ob-

TABLE I. Data on donor stumps and receptor trees. The records of total volume of dye intake are computed from the time of first application of dye to each stump. If starred (*), the records represent 264 hours, otherwise 252 hours

	DONOR STUMPS					RECEPTOR TREES DETECTED		
No.	Age (yrs.)	Diameter i.b. (cm)	Basal area (cm²)	Sapwood area (cm²)	Total dye intake (l)	Distance from donor (m)	D.b.h. (cm)	No. of roots w/dye
3	63	33.0	855.7	243.1	3.54*	2.7	44	1
						3.2	44	1
6	53	25.9	526.8	152.3	6.95	0.8	19	4
						1.8	28	6
7	43	22.9	410.2	125.4	4.76*	—	None	—
8	30	20.3	324.1	75.9	3.35*	1.2	30	4
						1.6	25	1
10	56	29.5	681.3	252.9	12.33	—	None	—
11	59	33.5	882.2	313.4	7.15*	3.4	52	1
						3.9	56	1
12	55	22.9	410.2	162.1	9.98	2.6	40	5
13	44	19.3	292.4	85.1	3.86	2.8	47	1
						3.8	47	1
14	63	35.6	992.4	414.9	14.98	—	None	—
15	72	51.8	2,107.2	678.3	23.05	3.4	42	3
						4.3	40	2
Av.	54	29.5	748.3	250.3	9.00	2.7	40	2.4

servation period each potential receptor tree was periodically examined for the presence of dye.

THE STAND

The stand in which this work was done supported uneven-aged old-field pine, with a low mixed hardwood understory composed predominantly of white ash, *Fraxinus americana* L. Ground cover was sparse in some areas, and in others consisted of massed 3- or 4-year-old pine seedlings, dense mixed woodland ferns, or masses of low-growing poison ivy, *Rhus radicans* L.

The site elevation was approximately 600 ft above mean sea level, with a northwest exposure and a 10% slope. The topsoil was a brown sandy loam, 40 to 50 cm in depth, with stones from pebble- to boulder-size scattered throughout, and some evidence of a disturbed plow layer in the top 10 cm. The subsoil, apparently poorly drained, was a tight yellow-gray fragipan which graded into a weathered mica-schist at depths exceeding 1.0 m.

RESULTS

Before discussing the intake of dye through the 10 donor stumps, other observations should be summarized to indicate the extent of root grafting in the stand. To detect the presence of root grafts, several flaps of bark on every major root of each potential receptor tree were lifted periodically during the 10-day observation period. This examination disclosed that dye had moved, through existing natural root grafts, from 7 of the 10 donors to 13 receptors through 31 major receptor roots (Table I). It was thus demonstrated that 7 of the donors were involved in at least 31 individual intraspecific grafts with the 13 receptors. Although no inference could be drawn as to the size or actual number of grafts transmitting dye from donors to receptors, other observations indicated that the amount of grafting thus demonstarted by dye transfer was underrepresentative. In some instances dye failed to move through large grafts between donors and nearby grafted neighbors, while the same donors were actively passing dye through other grafts. On one plot, where dye transfer had revealed 2 receptors, partial excavation disclosed a union of at least 6 trees with more than 35 separate intraspecific grafts. These observations indicated that some grafts were inoperative in the transfer of dye, and suggested the possibility that even the 3 donors from which no dye transfer had been detected were grafted to other trees in some degree. Another observation from the dye intake studies, to be discussed later, supported this conclusion.

During the 10-day observation period, and later, after the dye reservoirs had been allowed to dry up, the dye on the stump surfaces appeared to be concentrated in the heartwood region, with much less color in the sapwood. Investigation indicated that this differential surface concentration was attributable to 2 factors: 1) The more active movement of dye into and through the sapwood left less residual dye at the surface than was left at the static dye-wood interface of the heartwood, and 2) Exuded resin in the sapwood area was

TABLE II. Dye intake, expressed as milliliters per square centimeter of sapwood area, for 10 donor stumps. Computations are for 12-hour periods commencing at the time of application of dye to each stump. Field notes indicate that the few exceptionally high values (*) may be attributable in part to slow leaks in the stump collars

Stump	Successive 12-hour Periods After Injection																				
	0-12	12-24	24-36	36-48	48-60	60-72	72-84	84-96	96-108	108-120	120-132	132-144	144-156	156-168	168-180	180-192	192-204	204-216	216-228	228-240	240-252
3	3.91	1.68	0.56	1.12	0.56	0.56	0.56	0.56	0.56	0.00	0.56	0.56	0.56	0.00	0.56	0.00	0.56	0.56	0.56	0.00	0.56
6	3.84	3.30	4.39	2.75	2.75	2.20	2.20	2.20	2.20	2.20	1.65	1.65	1.10	1.65	2.20	1.65	1.65	1.65	1.65	1.10	1.65
7	4.15	*8.31	4.16	2.60	2.08	1.56	2.08	0.52	1.56	1.04	1.04	1.04	1.04	0.00	1.04	1.04	1.04	0.52	1.04	0.52	1.04
8	*9.49	2.71	2.71	2.03	2.71	2.03	1.36	1.36	2.03	2.03	0.68	0.68	2.03	1.36	1.36	1.36	2.03	0.68	1.36	1.36	1.36
10	*9.84	*9.41	4.70	2.99	0.00	1.71	1.28	1.71	1.71	1.71	0.86	1.71	0.86	1.28	1.28	1.71	0.86	1.71	1.28	1.28	0.86
11	1.79	2.24	1.79	2.24	1.79	1.34	1.34	0.89	1.34	0.45	0.45	0.89	0.89	1.34	0.00	0.00	0.89	0.45	0.45	0.89	0.45
12	4.83	3.62	4.83	3.22	3.62	*8.45	2.82	2.82	2.82	2.82	2.01	2.41	2.01	2.01	2.01	4.02	0.00	1.61	2.01	1.61	2.01
13	4.37	3.82	4.37	2.73	2.73	2.18	2.18	1.64	2.73	2.18	1.64	1.64	1.09	1.64	2.18	4.37	0.00	0.00	1.09	0.00	2.73
14	1.90	*9.88	4.18	2.28	2.28	1.90	1.52	1.52	0.76	1.14	0.76	1.14	0.38	0.76	1.14	1.14	0.38	0.76	1.14	0.38	0.76
15	1.48	2.46	2.95	1.48	1.48	1.97	1.97	1.48	1.97	1.97	1.48	1.48	0.98	1.48	1.48	0.98	1.97	0.98	1.48	1.48	0.98
12-hr. total	45.60	47.43	34.64	23.44	20.00	23.90	17.31	14.70	17.68	15.54	11.13	13.20	10.94	11.52	13.25	16.27	9.38	8.92	12.06	8.62	12.40
24-hr. total		93.03		58.08		43.90		32.01		33.22		24.33		22.46		29.52		18.30		20.68	

abundant. The resin, being impervious to the dye, remained clear while submerged, and became translucent when exposed to air, thus affording the sapwood surface a much lighter color than that of the heartwood.

Immediately following the 10-day observation period, 10-cm thick discs were cut from the tops of a number of the donor stumps. At that distance below the stump surface there was no dye in the heartwood, while the sapwood was heavily and uniformly stained (Fig. 2). In the light of this evidence that the entire sapwood area is involved in downward translocation of dye, and to make comparable the data from stumps of different sizes, intake rates will be expressed as milliliters of dye per square centimeter of sapwood area per unit time (ml/cm² spwd/t). For comparison, the total dye-intake for each donor is expressed in liters in Table I.

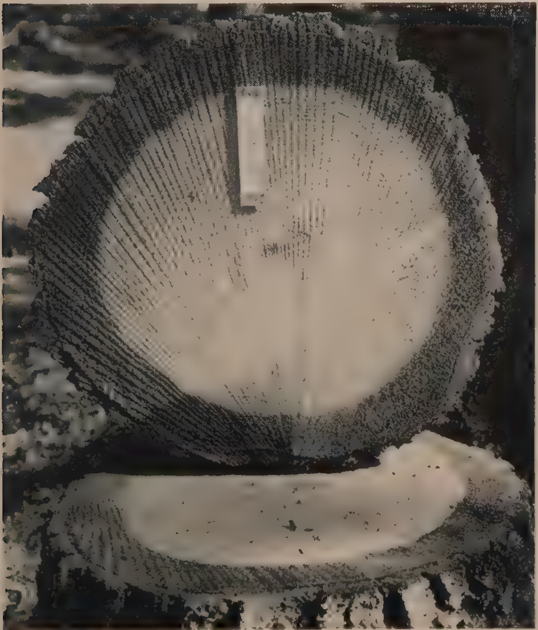

FIG. 2. Heavily stained sapwood 10 cm below the surface of a donor stump which had been injected with 0.15% aqueous acid fuchsin.

The data indicate that white pine stumps take in dye most rapidly during the first day after injection. Although approximately 12 hours passed from the time dye was placed on the first stump to the time it was applied to the tenth stump, the dye intake records in Table II have been adjusted to represent the intake per unit area of sapwood during successive 12-hour periods following application of dye to each stump. These data, when plotted for successive 24-hour periods following application of dye (Fig. 3), show clearly the initial surge of intake during the first 24 hours, with a subsequent decline until, after the sixth or seventh day, the intake rate became relatively steady.

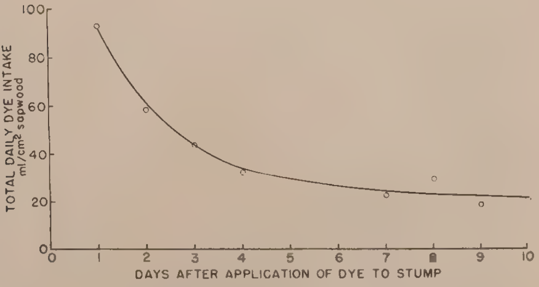

FIG. 3. Total daily dye intake for 10 donor stumps during the 10 days immediately following injection.

The complexity of the interactions of living trees with their environment makes accurate correlation difficult. The response of transpiring trees to their environmental conditions is of par-

TABLE III. Records of daily and nightly dye intake, expressed as milliliters per square centimeter of sapwood area, for the period commencing at 8 a.m. July 16, and ending at 8 p.m. July 26, 1957. Days (D) are from 8 a.m. to 8 p.m., and nights (N) are from 8 p.m. to 8 a.m. Field notes indicate that the exceptionally high readings (*) may be attributable in part to slow leaks in the stump collars

Date (July 1957)	Stump Number										Total (D)	Total (N)	Average (D)	Average (N)
	3	6	7	8	10	11	12	13	14	15				
16 D	1.68	3.84	8.31*	2.71	9.84*	2.24	4.83	4.37	1.90	1.48	41.20		4 120	
N	0 56	3.30	4.16	2.71	9.41*	1.79	3 62	3.82	9.88*	2.46		41.71		4.171
17 D	1 12	4 39	2 60	2 03	4.70	2.24	4.83	4.37	4 18	2.95	33.41		3 341	
N	0.56	2 75	2 08	2.71	2.99	1.79	3 22	2.73	2.28	1.48		22 59		2 259
18 D	0 56	2.75	1.56	2.03	0 00	1.34	3.62	2.73	2 28	1.48	18.35		1 835	
N	0 56	2 20	2 08	1.36	1.71	1.34	8 45*	2.18	1.90	1.97		23 75		2 375
19 D	0.56	2.20	0 52	1.36	1 28	0.89	2.82	2.18	1.52	1.97	15.30		1 530	
N	0.56	2 20	1.56	2.03	1.71	1.34	2.82	1.64	1.52	1.48		16 86		1 686
20 D	0.00	2 20	1 04	2.03	1.71	0.45	2 82	2 73	0.76	1.97	15 71		1 571	
N	0 56	2 20	1.04	0.68	1.71	0 45	2.82	2.18	1.14	1.97		14 75		1.475
21 D	0 56	1.65	1.04	0.68	0.86	0.89	2.01	1.64	0 76	1 48	11 57		1.157	
N	0.56	1.65	1 04	2.03	1.71	0.89	2 41	1 64	1.14	1.48		14 55		1.455
22 D	0 00	1 10	0.00	1 36	0 86	1.34	2 01	1.09	0 38	0 98	9 12		0 912	
N	0.56	1.65	1.04	1.36	1.28	0.00	2.01	1.64	0.76	1 48		11 78		1 178
23 D	0.00	2.20	1 04	1 36	1 28	0 00	2 01	2 18	1.14	1 48	12.69		1.269	
N	0.56	1.65	1.04	2.03	1.71	0.89	4.02	4.37	1.14	0.98		18.39		1 839
24 D	0.56	1.65	0 52	0.68	0 86	0.45	0 00	0 00	0.38	1 97	7 07		0.707	
N	0.56	1.65	1.04	1.36	1.71	0.45	1.61	0.00	0.76	0 98		10 12		1 012
25 D	0 00	1.65	0.52	1.36	1.28	0.89	2.01	1.09	1.14	1.48	11 42		1 142	
N	0.56	1.10	1.04	1.36	1.28	0.45	1.61	0.00	0.38	1.48		9.26		0.926
26 D	0 00	1.65	0.52	1.36	0 86	0.89	2 01	2.73	0.76	0.98	11.76		1.176	
Total (11 days)	5.04	25 28	17.67	16.96	23.53	11.62	28 97	25 11	15.20	18.22	187.60	Total 11 days, 10 trees		
Total (10 nights)	5.60	20.35	16.12	17.63	25.22	9.39	32 59	20.20	20.90	15.76	183.76	Total 10 nights, 10 trees		
											371.36	ml/cm² spwd (Grand Total)		
Av. (11 days)	0 458	2.298	1.606	1.541	2.139	1.056	2.633	2 282	1 381	1 656				
Av. (10 nights)	0.560	2.035	1.612	1.763	2,522	0.939	3 259	2.020	2.090	1.576				

ticular interest, however, in this study where conditions conducive to higher transpiration might reasonably be expected to increase the rate at which dye moved from donor stumps to their grafted neighbors.

During the first 2 days of observations, bihourly readings of dye-level were made to detect any marked periodicity or diurnal fluctuation in intake rate. No such variation occurred. The bihourly readings have been consolidated and are presented, with the remainder of the dye intake measurements, in Table III. The average daily and nightly volumes of dye intake, for the periods 8 am to 8 pm, and 8 pm to 8 am respectively, are shown graphically in Fig. 4. Although the amount of dye taken in during the night period exceeded that for the day period on 7 out of 10 days, the difference between the day and night averages over the 10-day period is not statistically significant.

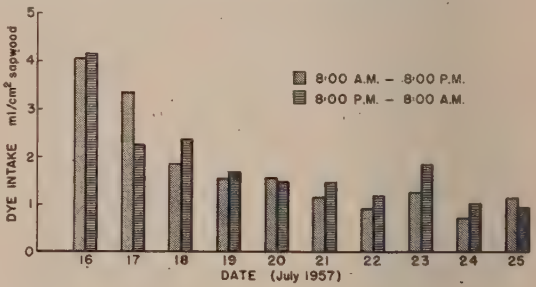

FIG. 4. Average daily and nightly volumes of dye intake for the 10 donor stumps during a 10-day period.

Viewed in the light of concurrent weather records obtained from the Shattuck Observatory at Dartmouth College, however, the data in Table III show what appears to be a marked response to weather conditions. In plotting the average volume of dye taken in daily by the 10 donor stamps (Fig. 5a), it was noted that, superimposed upon a generally downward trend, there was a definite increase in the volume of dye taken in by the stumps on July 23rd. Temperature, relative humidity, wind velocity and precipitation records plotted for the same 10-day period are shown in Fig. 5b and c. July 23rd followed a dry period of several days, but was immediately preceded by 2 days when light rains fell. The 23rd was rainless, with a breeze averaging 6.3 m.p.h., and uniformly low relative humidity throughout the day. One stump took in less, 2 took in the same volume, and 7 took in greater volumes of dye than on the 22nd (Table III). The fluctuation in average dye intake from 2.09 ml/cm² spwd on the 22nd, to 3.11 on the 23rd, and back to 1.72 on the 24th suggests more than a coincidental correlate to concurrent weather conditions. The dye was apparently taken up at rates which reflected physiological responses of the intact trees to which the stumps were grafted.

DISCUSSION

Two characteristics of the intake of dye through the donor stumps, as summarized in Table I, are notable: 1) the total intake volume varied considerably from stump to stump, without any apparent relationship to the sapwood areas of the individual stumps, the number of receptor trees detected, or the number of receptor roots receiving dye from the donors; 2) the rates at which dye was taken in during the 10-day period are very low when compared to those observed by other tree injection workers.

The stump to stump variation, 3.35 l to 23.05 l for the 10-day period, could be a reflection of the total number and actual sizes of the grafts involved, information not available from the present data; or it may indicate that the movement of dye into stumps is controlled, at least in part, by biophysical mechanisms not now apparent. It must be recognized that the 2 roots involved in any intraspecific, or interspecific, graft (i.e., in contrast to self-grafts) are probably genotypically unlike. Perhaps such pairs of genotypes are characterized by various degrees of compatibility, and it would seem logical to expect differences in the mechanics of transport on this basis.

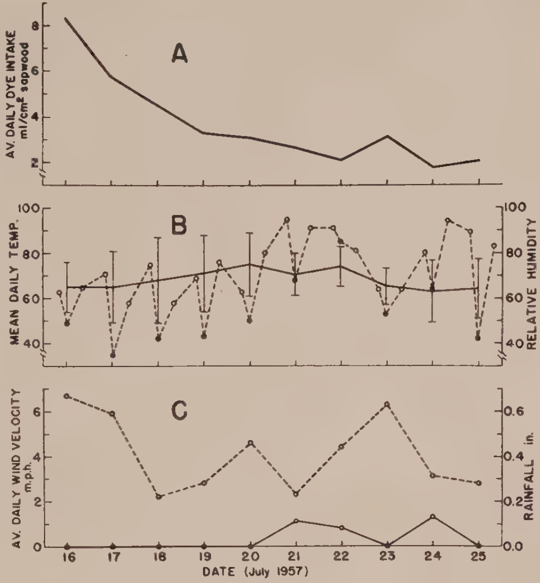

FIG. 5. The average volumes of dye taken in daily by 10 stumps of eastern white pine, as related to concurrent weather records. A) Average daily dye intake in ml/cm² of sapwood. Each daily record represents the average for 10 stumps. Calculations are based on 24-hour periods commencing at 8 a.m. B) The dotted line connects relative humidity percentages recorded daily at 8 am, 12 m and 8 pm. The midday readings are indicated by blackened circles. The solid line represents mean daily Fahrenheit temperature, with daily range indicated by vertical brackets. C) The dotted line connects average daily wind velocities expressed in miles per hour. Averages were computed from 12 hourly readings taken from 8 am to 8 pm daily. The solid line connects records of total daily rainfall recorded in tenths of an inch.

In many instances dye moved, in quantity, for short distances along roots of donor stumps, stopping unexplainably. Other donor roots received no dye. The possibility suggested itself, at first, that any downward movement of dye, into a root of a donor stump, might indicate the presence of a graft somewhere along the root involved; but then grafted roots were found into which no dye had moved, and ungrafted roots were found which contained dye. Such behavior indicates that even isolated roots on a single donor stump may be influenced by different sets of factors, one of which may be soil moisture. Roach (1939) cites one instance in which dye, injected into an apple tree growing in a soil wet near the surface, but dry deeper down, penetrated to the tips of roots in the dry soil but did not penetrate very far into roots in the wet soil. The exceptionally dry summer when the present work was done, like the period described by Roach, was broken, only occasionally, by light rains capable of partially wetting the soil; and the differential movement of dye may have been a reflection of the moisture stress of the donor roots. Commenting further on his observation, Roach says, "The movement of dye to the very tips of the roots suggests that some of the water in which it was dissolved must have left the root-tip and entered the soil, since water usually moves more freely than the dye dissolved in it." A similar mechanism was demonstrated by Hunter and Kelly (1946) and showed that roots of corn are able to elongate into, and build up the soil moisture content of, air dry soil.

Thus the anomalous uptake of dye by the 10 white pine stumps may reflect the operation of a complex of factors including: 1) the total number and actual sizes of grafts involved, 2) degrees of anatomical or biophysical compatibility influencing transport between grafted genotypically unlike roots, and 3) microenvironmental conditions influencing transport through individual roots.

No statement of the rate of dye intake through pine stumps has been seen by the writer. Workers with tree injections, however, mention intake rates for various materials injected into the trunks of intact trees. Greenidge (1955a), having injected 0.15% aqueous acid fuchsin into transpiring trees of *Acer saccharum, Ulmus americana, Populus balsamifera* and *Fagus grandifolia,* with breast height diameters from 5 to 10 in., reported initial intake rates of 1.8, 6.0, 1.7 and 6.6 l/hr respectively. Craighead and St. George (1938), in injecting numerous chemicals into pine, spruce, fir, oak, hickory and yellow poplar, observed intake rates of from 1 to 2 gals (3.8 to 7.6 l) in from 1 to 3 hr under favorable conditions. Rumbold (1920, Fig. 4) shows a curve, very similar to that in Fig. 3, representing water intake through paired holes for 6 intact chestnut trees during 7 days in July 1913. The mean volume of water and numerous other solutions taken in by each of 156 trees during that month was 201 ml/day. The highest rate, that for June, was 299 ml/day. True, *et al.* (1955) concluded that a water intake rate of approximately 1/day/diameter-inch could be expected through the tops of freshly cut oak stumps. Either, or both, of two factors, it seems, could account for the relatively low intake rate observed in the 10 white pine stumps: 1) It could be characteristic of white pine, and of movement through tracheids or, 2) It could reflect minimal transpiration of the intact receptors during an exceptionally dry summer.

Other workers have noted that materials injected into woody stems are apparently taken in rapidly at first, with the rate tending to become slower and comparatively constant. Fraser and Mawson (1953), in discussing the injection of rubidium-86 into yellow birch, state, "The decrease in movement that followed the rapid initial uptake and movement of the isotope in healthy trees may have resulted from a lowered tension in the transpiration stream as the solution was taken up from the trough."

Stoddard and Dimond (1949) describe a portion of a United States Department of Agriculture film dealing with Dutch elm disease thus:

> The trees [elms] were stripped of bark, fitted with a metal collar after the manner of Shevyrev [1894], and the suspensions [carbon particles and yeast cells dyed with haematoxylin] poured into the funnel-shaped reservoir. Immediately upon making the chisel cuts, the wood into which the fluid was absorbed became colored by the absorbed suspension, the coloration moving initially up and down the stem from the point of entry at the rate of three inches per second through conductive wood. Such entry of liquid into the stem was in response to the pressure differential between the water columns in the tree and the atmosphere outside. When the pressure differential disappears, this surge ceases. Then fluid moves into the tree in response to the tranpirational loss from the leaves, this pathway of water movement offering less resistance to flow than the pathway through the roots from the soil.

In their work with 15 oak stumps, True, *et al.* (1955) found that the intake of water by stump tops was greatest during the first 24 hours, and that stumps of trees a foot or more in dbh continued to absorb water for as long as 5 days, with the rate of absorption greatly reduced after the first day. Rumbold (1920) found that the typical curve of intake, for numerous substances injected into chestnut trees, reached its highest point the first 24 hours after injection, then decreased steadily. Rankin (1917), having injected chestnut trees with lithium nitrate solutions, reported that the greatest intake was during the first 2 days, and had practically ceased after the fifth day. It is noteworthy that, although True and his colleagues (1955) made their injections through stumps for downward translocation in Oak, and Rumbold (1920) and Rankin (1917) made theirs through holes for upward translocation in chestnut, the initial surge occurred in all instances. The results of the present experiment show that a similar initial surge in intake rate is also characteristic of the movement of dye solution into the sapwood of freshly cut white pine stumps, the roots of which are grafted to nearby intact trees. In white pine, as in other species, it can probably be attributed to an equilibrium adjustment occasioned by the rupturing of a closed system which has been under tension. Following the initial adjustment, the rate at which dye solution moves from cut stumps, through root grafts, and up into other members of the root graft complex probably reflects the transpiration rate of the intact receptors. It seems certain, however, that such reflection must be modified, anatomically, by the number and size of grafts involved; and the possibility of biophysical influence incident to the vascular union of genotypically unlike organisms should not be overlooked.

That the weather influences the rate at which injected materials are taken up by trees must have been recognized by many investigators, but the complexity of the relationship practically defies analysis. Pertinent observations in the literature are rare and usually generalized. Greenidge (1955b), after injecting several hardwood species during his study of stretched water columns in transpiring trees, concluded that, "Rates of uptake varied widely within and between species, and were correlated with a number of factors including crown class, size of bole and crown, time of day, relative humidity, wind velocity, temperature, cloud cover, immediate and recent pre-injection history and perhaps other variables." Rumbold (1920) presents a compilation of weather records from April through October, with the average daily volume of solution absorbed by a large number of chestnut trees computed for each month. She notes that, where absorption of solution is concerned, the number of rainy days was more influential than the amount of rain.

The relationship between the weather factors and the increased dye-intake on July 23rd seems clear (Fig. 5). Conditions conducive to an increased transpiration rate included an extended dry spell, then 2 days with light rains totaling 0.19 in (4.8 mm) and, on the day showing an increase in average dye intake, no rain, a 6.3 mph breeze, and uniformly low relative humidity. The increase observed in the average volume of dye intake would seem to support the concept that grafted trees constitute a physiological union the whole of which is effected by environmental changes involving any part. Wichmann (1925) implied as much in making the observation that, "When a whole group of densely spaced trees dies in quick succession following a lightning stroke, it is logical to think that, because their roots are grafted, they react as a physiological entity."

In the 18-hour period during which bihourly readings of dye intake were made, no evidence of periodicity occurred. The 10 stumps exhibited different but uniform rates of intake. It is difficult to understand why, during 10 days of daily and nightly observations, there was no evidence of a normal daily march of transpiration (Fig. 4). Rumbold (1920) states that, in her injections of some 156 chestnut trees, "The hourly intake was not measured, but experience confirmed Shevyrev's [1894] observations that the intake by day was greater than by night." Shevyrev (1894) reported a night intake rate, for dye injected into transpiring trees through chisel cuts, of 11 ml/hr, compared to a day rate of 33 ml/hr. Dole (1924) concluded from numerous observations of 6- and 8-year old potted white pine trees, under greenhouse and field conditions, that in the normal march of transpiration a maximum rate is reached at 1 pm, and the minimum occurs from 11 pm to 3 am.

July of 1957 started with a deficit of more than 5 inches (12.7 cm) in cumulative precipitation in Hanover, N.H. One explanation for the lack of expected periodicity which suggests itself is that transpiration during this unusually dry summer may have been minimal, possibly predominantly cuticular, thus minimizing differences between day and night rates.

Another indication of the influence of root grafting on the intake of dye through stumps may be contained in the present data. True, *et al.* (1955) found, with oaks, that the persistence of living transpiring trees, grafted to the cut stump, caused both an increase in and a prolongation of the intake of azosulfamide dye, and of copper sulfate solution. They found that 7 isolated oak stumps, with neither sprouts nor root grafts, absorbed the solutions the first day, and little or none thereafter. Two stumps, with companion sprouts, absorbed about twice as much dye during the first 2 days as did 3 stumps with neither sprouts nor root grafts; and then intake ceased. Three stumps with both sprouts and root grafts, however, took in solutions most rapidly initially, and intake continued during the entire 7-day period of observation. On the basis of these observations they suggest that, "Perhaps the prolongation of uptake alone may serve as one indication of root graft in the case of cut stumps lacking standing companion sprouts."

The data plotted in Fig. 6 show a continued accumulation, over a 10-day period, for the 10 white pine stumps on the experimental site. It was pointed out earlier that 7 of the 10 stumps were known to be grafted, and chances seem good that the others, too, were grafted in some degree. Thus the continued dye-uptake was associated with root grafting and adds support to the proposal of True and his colleagues. A complementary experiment with a group of isolated stumps could shed further light on this point.

SUMMARY

In the light of recent investigations, it appears that wherever a forest tree species occurs in groups, from clumps of 2 or 3 trees to extensive

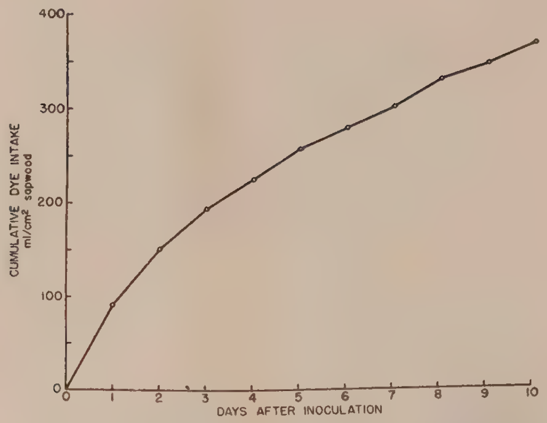

Fig. 6. Cumulative volume of dye taken in, during the 10 days following injection, by 10 donor stumps, 7 of which are known to have been root-grafted to intact trees.

relatively pure stands, natural root grafts are probably present. The forest, therefore, is not composed entirely of competing "individuals" occupying the same area and dependent upon the same physical factors, but contains much-grafted tree unions capable of direct physiological interaction. Observations of some such interaction between eastern white pine trees in an uneven-aged (54-yr av.) old-field stand in New Hampshire are presented here.

Acid fuchsin dye, introduced through the tops of 10 freshly cut pine stumps, was observed to enter the sapwood of the stumps and to move, through natural root grafts, to nearby intact trees. From 7 of the 10 treated stumps, dye moved into 13 adjacent receptor trees through 31 major roots.

Dye was taken in most rapidly during the first 24 hours, and intake continued, at a diminishing rate, for 9 subsequent days of observation. It is suggested that uptake which continues for more than a day or two may be, in itself, an indication that a stump is grafted to adjacent intact trees. Repeated sprouting of tree stumps, and continued growth of girdled trees, phenomena sometimes encountered in forest management, probably also indicate the presence of natural grafts.

Following a prolonged dry period, meteorological conditions which should have been conducive to increased transpiration by the intact trees, coincided with increased dye intake by 70% of the stumps. This apparent relationship suggests that trees may be influenced by environmental factors not only directly, but also indirectly through their grafted companions.

No periodicity or diurnal variation in intake-rate was demonstrated. It is suggested that an unusually dry summer (1957) may have resulted in minimal transpiration, essentially cuticular, and in absence of the normal daily march.

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THE ECOLOGY OF A BIOTIC COMMUNITY CONSISTING OF ALGAE AND BACTERIA

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Two important areas for the application of biological processes are the reclamation of water and organic nutrients from waste waters and the complete control of enclosed environments. The former may be accomplished through the agency of biotic communities consisting of algae and bacteria grown in especially designed lagoons known as "high-rate oxidation ponds." These ponds have been described by Oswald and his colleagues (1954, 1957, and 1958). The biological control of enclosed environments, such as in atomic submarines or in space vehicles, may also be brought about through the collective activity of algae and bacteria and has been described by Golueke and Oswald (1958).

The successful application of a biological process to such widely divergent and, paradoxically, closely related functions as the control of the environment in a space vehicle and the treatment of wastes in a high-rate oxidation pond requires an extensive knowledge of the ecology of the organisms involved in the process. This is true because effective biological control requires an optimum relationship between the environment and the biotic community concerned, and this can be accomplished only by providing proper environmental conditions. To establish such a relationship, it is necessary to know the nature and extent of the influence of the principal environmental factors involved. Among the key factors to which an algal-bacterial community is subject, whether in an oxidation pond or in a space ship, are carbon dioxide concentration, light intensity and length of duration of light per day, length of growth period, and temperature. In a space ship these factors can be regulated mechanically, and in an oxidation pond, by engineering and geographical location.

Although much has been written on the effect of the key environmental factors on individual algal species, there is a paucity of information in the literature on the effect of these environmental factors, either individually or collectively, on such organisms when living as members of a biotic community. Inasmuch as the influence of these factors are modified by the collective action of different types of organisms living together in the same community, and by the nature of the action of one group upon the other, information gained from studies of an organism grown as a pure culture cannot be applied unequivocally to the same organisms when living as a member of a biotic community.

This paper treats that part of an investigation on the biological control of enclosed environments which deals with the influence of certain environmental factors in determining the nature and over-all activity of climax associations of algae and bacteria resulting from the application of a given set of factors.

In the description to follow, the term "culture" will be used synonymously with "biotic community," inasmuch as the microorganisms were grown in a prepared nutrient medium under controlled conditions.

The author wishes to express his appreciation for counsel given him by Dr. W. J. Oswald, Dept. of Civil Engineering and School of Public Health, University of California, Berkeley.

MATERIALS AND METHODS

A mixed culture of Chlorella, Scenedesmus, and various unidentified bacteria was used in the present study to approximate the type of culture employed in treating sewage in high-rate oxidation ponds or in controlling enclosed environments. Ideally, communities used in the two processes should be able to operate at high efficiencies under a wide spectrum of environmental conditions, because the key environmental factors can be only partially controlled in an oxidation pond, and, in a space vehicle, control may be interrupted by mechanical malfunction or by loads exceeding the capacity of the control equipment. Therefore, a biotic community consisting of at least two algal cultures and several bacterial species is more appropriate than a pure culture, since the range of optimum conditions for a community is as broad as the total spread between the optimum limits of all of the groups involved. On the other hand, the optimum range for a pure culture is limited to that of a single species. Moreover, the algal and bacterial groups studied were those capable of functioning uniformly well within the temperature range 20° to 42°C. Such organisms were selected because the biological control of enclosed environments requires organisms adapted to a range of temperature, the upper limit of which is higher than optimum for most commonly occurring strains. A full description of the development of the culture as well as of the procedure followed in maintaining a uniform stock culture of the organisms is given in another report (Golueke and Oswald 1958).

The experiments were conducted with the use of continuous automatic growth units, which have been described in detail by Oswald (1957). Six of the units were operated in parallel during each experiment. Each unit was equipped to maintain continually a preset detention period,[1] temperature, light duration, light intensity, and rate of gas flow. Provision was made for varying the strength and composition of both the nutrient sewage and of the gas used for mixing and as a source of carbon dioxide. The growth units were designed so that experiments could be continued indefinitely, although a period of ten days usually was more than ample for the attainment of a "steady-state" or climax.

Continuous cultures were used because they duplicate more closely the conditions to which such cultures would be subjected in their application. Moreover, with continuous cultures, it is possible to set up and maintain indefinitely predetermined climax conditions, and thus make possible extended studies on the over-all characteristics of the associations which result. A disadvantage involved in the use of batch cultures is that any sampling done during the course of the experiment may bring about significant variations in the results because of the gradual loss in volume due to the removal of the samples. Although this can be overcome by using multiple replicates of batch tests, the latter technique is cumbersome and subject to inaccuracies.

Photosynthetic efficiency, as used in this paper, is the over-all light energy conversion efficiency expressed as per cent. It is based upon the ratio of chemical energy permanently fixed in the form of algal material each day to the visible light energy absorbed by the cultures during the day. Determinations of this over-all photosynthetic efficiency were made according to the procedure described by Oswald (1957).

Unless otherwise stated in later descriptions of individual experiments, each experiment was initiated as follows. Four liters of algal culture were removed from the stock culture and poured into an 11-liter Pyrex bottle. Two liters of raw sewage, strained through glass wool, were added to the culture. The resulting suspension was enriched with urea (0.3 g per liter of suspension) and an aliquot poured into each of the growth units. The cultures were illuminated by a single lamp for a period of two days to permit the algae to become adjusted to the radiation of the fluorescent lamps. At the end of this period, the light was increased or diminished according to the conditions of the experiment. The cultures were not placed on detention period, i.e., feeding was not initiated until the end of the second day. At that time they were subjected to the conditions of the experiments for a period varying from 8 to 10 days. During the course of the experiment, daily observations were made of algal population counts and of the packed volume of the cultures.

Domestic sewage enriched with 0.3 g of urea per liter was selected as a nutrient for the cultures because such a mixture approximates the medium which would be available in their application in oxidation ponds and in space ships. This nutrient differed from the "stock" nutrient used in initiating the experiment in that the sewage was first sterilized in an autoclave, and a solution of urea in distilled water, sterilized by passage through a Seitz bacterial filter, was subsequently added. Urea was used in preference to other nitrogen sources because it eliminated the problem of phospate precipitation which often accompanies the use of ammonium phosphate, and the pH problem which characterizes media containing ammonium sulfate or nitrates. The concentration of urea and the composition of the medium were based upon the results of experiments reported in an earlier publication (Golueke and Oswald 1958).

Except for the factor or factors being varied, "standard" conditions for the experiment were: detention period, 3 days; CO_2 concentration, 2%; light energy input, 28.6 cal/liter/min; light duration, 60% (expressed as per cent periodicity; i.e., 100 times hours of light divided by 24); and temperature, 30°C. Gas was passed through each culture at 0.2 cu ft per hour. Although no attempt was made to control the pH of the cultures, it rarely varied beyond the range 6.5 to 7.5.

RESULTS

Photosynthetic Efficiency

The effect of detention period upon the photosynthetic efficiency of the algal population was modified by the temperature at which the cultures were grown, as is shown in Figure 1. Maximum efficiencies were attained at the 2-day detention period when the cultures were maintined at 23° and 26°C. Efficiency was lowest when the detention period was 1 day, and the temperature, 23°C. When the temperature was increased to

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[1] Detention period $= D = V/Q$, where D is detention period in days, V is the volume of the growth unit, and Q is the displacement volume per day.

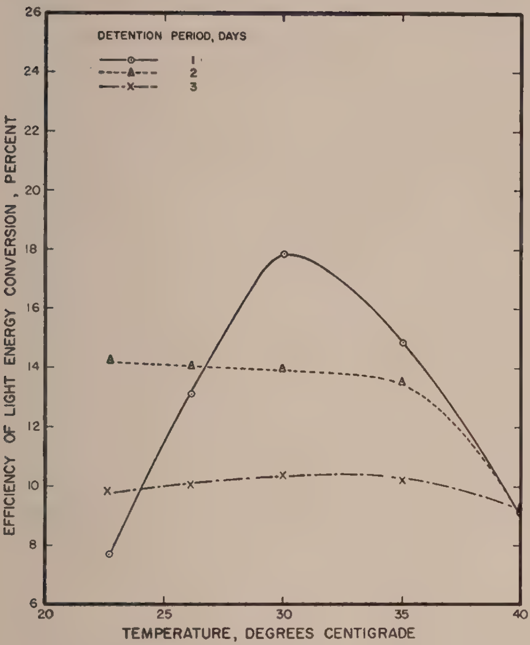

FIG. 1. Photosynthetic efficiency as a function of temperature and detention period.

26°C, the culture operating on a 3-day detention period had the lowest efficiency, while that on the 1-day period was only 1% less than the maximum attained at the 2-day detention period. At temperatures of 30° and 35°C, efficiency decreased with decrease in detention period from a maximum at the 1-day period to a minimum at the 3-day period. Detention period (1-3 days) had but little effect on efficiency at 40°C.

The mutual effect of periodicity and CO_2 concentration may be judged from the data listed in Table I. According to the data, periodicity within the range studied had but little effect upon the efficiency of cultures at concentrations of CO_2 of 0.03, 1, and 2%. At concentrations of 3 and 4%, however, efficiency increased from 10 and 12% at a periodicity of 40% to 14 and 15% at a periodicity of 80%.

TABLE I. The effect of concentration of CO_2 upon the over-all photosynthetic efficiency as modified by periodicity. The values given express the per cent over-all efficiency of the culture. Unless otherwise indicated in the table, detention period was 2 days, temperature, 30°C, and light energy input, 28.6 cal/liter/min

CO_2 (%)	PERIODICITY (%)				
	40	50	60	70	80
0.03	5.7	7.3	6.9	6.6	6.4
1.0	13.5	15.2	12.6	15.0	13.0
2.0	12.1	14.3	12.0	14.7	13.0
3.0	11.9	12.9	13.0	14.1	14.9
4.0	10.1	12.8	13.3	13.4	14.1

The data listed in Table II show that the efficiency of the cultures was markedly affected by rate of light energy input, while the degree of influence was, in turn, determined by the concentration of CO_2. Efficiencies were lowest at the minimum input of light energy (1.8 cal/liter/min), ranging from 0.5% to 7% at CO_2 concentrations of 0.03% and 3% respectively (Table II). The extent of gain in efficiency upon increasing the light energy input from 1.8 to 8.1 cal/liter/min declined as CO_2 concentration was increased from 0.03% to 4%. Increasing the light input beyond 8.1 cal/liter/min resulted in a continued decline in efficiency at all of the concentrations of CO_2, ranging from a maximum decrease of 57% with increase in light from 8.1 to 28.6 cal/liter/min at a CO_2 concentration of 1%, to a minimum of only 2½% at a 4% concentration of CO_2 within the same range of light energy input.

TABLE II. The effect of concentration of CO_2 upon the over-all photosynthetic efficiency as modified by light energy input. The values given express the per cent over-all efficiency of the culture. Unless otherwise indicated in the table, detention period was 2 days; temperature, 30°C; and periodicity, 60%

CO_2 (%)	LIGHT ENERGY INPUT: CAL/LITER/MIN				
	1.8	8.1	14.5	21.1	28.6
0.03	0.5	12.3	9.1	7.7	6.9
1.0	6.2	23.4	17.1	13.8	10.1
2.0	6.4	20.8	17.5	14.2	12.0
3.0	7.0	15.2	16.8	13.1	11.5
4.0	5.8	14.6	13.1	12.1	10.9

Cell Concentration

The combined effect of CO_2 concentration and detention period on total cell concentration is indicated in Figure 2. At all detention periods a fivefold increase in cell concentration accompanied the change in concentration of CO_2 from 0.03% to 1%. Advancing the CO_2 concentration from 1% to 2% resulted in a second increase of about 170% at the 2-day period, and only 5-10% at the 3 to 5-day periods. At the 1-day period, on the other hand, cell concentration dropped linearly as the concentration of CO_2 was changed from 1 to 3%, and continued to decline, until at 4% CO_2 the number of cells was less than at 0.03% CO_2. Cell concentrations dropped about 40% with increase in CO_2 from 2 to 4% at the 2-day detention period, and about 20% at the 3, 4, and 5-day periods.

The combined effects of concentration of CO_2

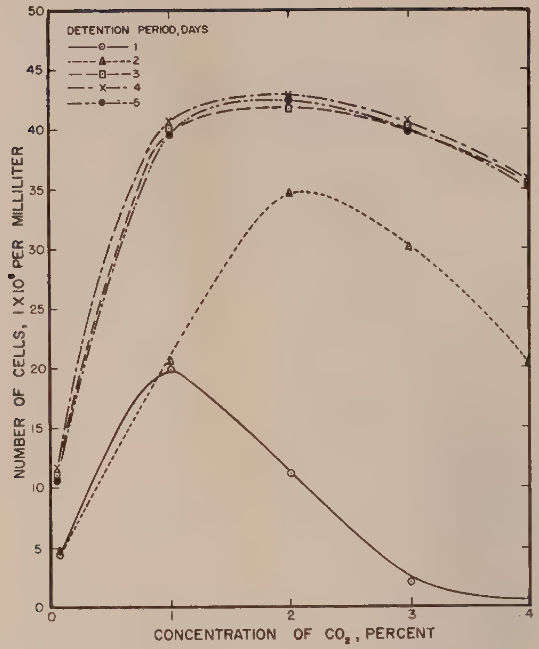

FIG. 2. The relation between concentration of CO_2, detention period, and population density.

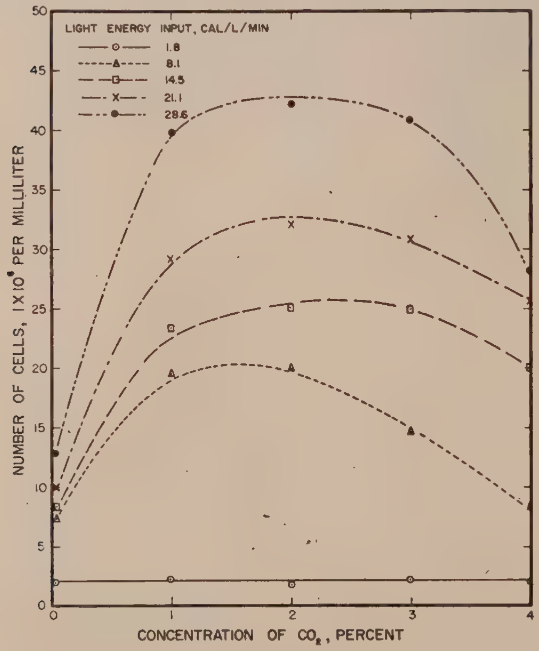

FIG. 3. The effect of light energy input and concentration of CO_2 upon the total concentration of algal cells.

and of rate of light energy input are indicated in Figure 3. At a light input of 1.8 cal/liter/min, increasing the CO_2 concentration had little or no effect upon the number of algae, and the total concentration of cells remained small, i.e., about 2 x 10^6 cells per ml. The effect of the higher CO_2 concentrations became more pronounced upon increasing the light input to 14.5 or more cal/liter/min. The extent of the increase was in proportion to the increase in light energy. The per cent increase in number of cells accompanying increase in CO_2 concentration from 0.03 to 1% was about 170% at an energy input of 14.5 cal/liter/min to about 210% at 28.6 cal/liter/min. Cultures receiving a light energy input of 8.1 cal/liter/min were characterized by a progressive drop in population at concentrations of CO_2 exceeding 1%, until at a concentration of 4% the cell concentration was the same as at 0.03% CO_2. At light energy input rates of 14.5 to 28.6 cal/liter/min, increasing the CO_2 concentration from 1% to 3% resulted in little or no additional increase in cells. Raising the CO_2 concentration from 3% to 4% brought about a 34% drop in cell concentration at 28.6 cal/liter/min and a 12% decline at 14.5 cal/liter/min.

Ratio of Scenedesmus to Chlorella

Regardless of variations in combinations of the environmental conditions within the limits investigated, *Chlorella spp* and *Scenedesmus spp* together always constituted almost 100% of the algal cells in the cultures, despite the fact that no attempt was made to exclude other groups. Because the cultures consisted almost exclusively of *Chlorella* and *Scenedesmus spp,* in reporting the results of the experiments, the relative proportions of one species to the other is indicated by expressing the incidence of Scenedesmus as the per cent of the total cell concentration represented by the group. The difference between 100% and the per cent Scenedesmus then equals the per cent of the culture as Chlorella.

The values for per cent as based upon total cell number are also applicable to per cent of the total dry weight of the culture. Although the Chlorella and Scenedesmus groups encountered in the present study differed morphologically, in that Chlorella cells were spherical, while those of Scenedesmus were either fusiform or prolate-spheroid, the relative dimensions of the two were such that on the average their volumes were similar. Chlorella cells varied in volume from $4\mu^3$ to $65\mu^3$ and averaged about $22\mu^3$. Scenedesmus ranged from $4\mu^3$ to $60\mu^3$, and averaged $21\mu^3$. Inasmuch as the specific gravity of the two is almost identical, cell for cell, the two groups were equal on a dry-weight basis; hence relative percentages of the total population reflect fairly closely relative percentages of total dry weight.

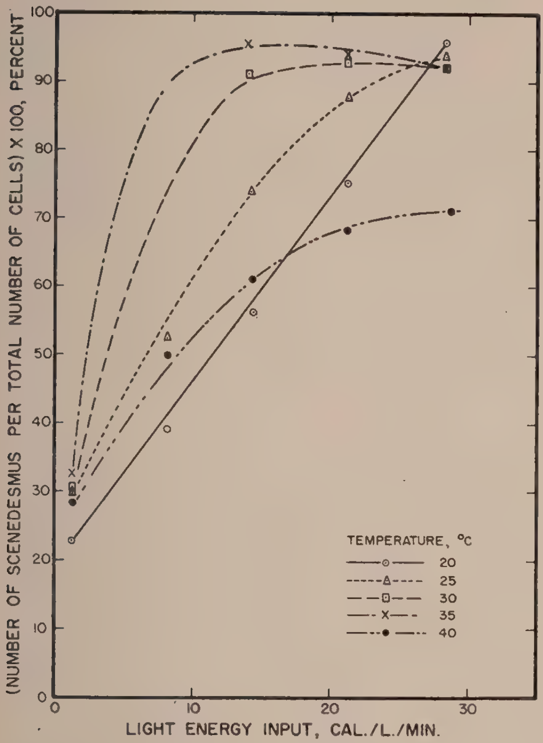

Fig. 4. The effect of light energy input and temperature upon the relative density of Scenedesmus.

Figure 4 illustrates the combined effect of light and temperature upon the composition of the total algal population. Inasmuch as Scenedesmus constituted only 24 to 34% of the algal cells, Chlorella was the dominant algal group when the light energy input was limited to 1.8 cal/liter/min and temperature was within the range 20° to 40°C. Increasing the light energy input increased the ratio of Scenedesmus to Chlorella at all of the temperatures tried; the degree of the increase, however, varied widely according to the temperature at which the culture was grown. At temperatures of 30° and 35°C, the maximum per cent Scenedesmus was reached at 14.5 cal/liter/min; however, at 20° and 25°C it was not attained until 28.6 cal/liter/min were applied. The gain was linear at 20°C and almost linear at 25°C. Scenedesmus never exceeded 70% at 40°C.

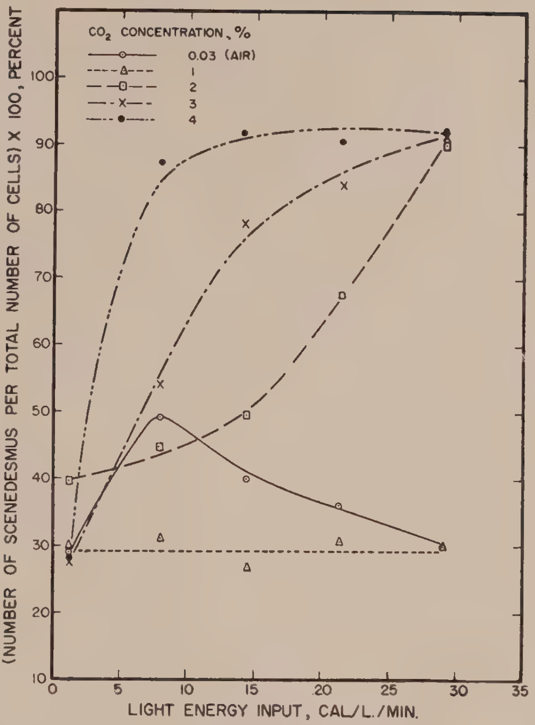

Fig. 5. The combined effect of concentration of CO_2 and light energy input on the relative density of Scenedesmus.

The influence of light energy input was markedly affected by CO_2 concentration, as is shown in Figure 5. A concentration of 0.03% CO_2 favored Chlorella, in that Scenedesmus constituted at the most about 48% of the culture at a light input of 8.1 cal/liter/min, and less than 40% at the other levels of light input. Chlorella outnumbered Scenedesmus 7 to 3 at all rates of light energy input when the concentration of CO_2 was kept at 1%. On the other hand, when the CO_2 concentration was increased to 4%, the concentration of Scenedesmus was greater than 87% of the total algal population at all input rates of light greater than 1.8 cal/liter/min.

The combined effect of light energy input and periodicity is indicated by the data listed in Table III. Light energy input together with periodicity exerted a pronounced effect on the relative numbers of the organisms. At a light energy input of 1.8 cal/liter/min, Scenedesmus constituted only 4% of the culture at a 40% periodicity; but as the

Table III. The effect of light energy input upon the relative numbers of Scenedesmus and Chlorella as modified by periodicity. The values given express the per cent of the total population as Scenedesmus. The detention period was 2 days; CO_2 concentration, 2%; and temperature, 30°C

Light Energy Input (cal/liter/min)	Periodicity (%)				
	40	50	60	70	80
1.8	4	13	19	32	66
8.1	19	38	43	46	82
14.5	40	47	49	73	90
21.1	59	65	73	84	92
28.6	65	80	86	90	91

length of light duration was extended, the number of Scenedesmus increased until at 80% periodicity Scenedesmus outnumbered Chlorella 9 to 1. Increasing the light energy input favored the growth of Scenedesmus at all of the periodicities with the result that at 28.6 cal/liter/min, Scenedesmus constituted from 66% of the culture at 40% periodicity to 96% at 80% periodicity.

The influence of light upon the ratio of Scenedesmus to Chlorella was modified by the detention period at which the culture was grown, as is shown in Figure 6. When the light energy input was restricted to 1.8 cal/liter/min, the per cent Scenedesmus increased from a low of 3.5% at the 1-day detention period to 70% at the 5-day period. Increasing the light energy input to 8.1 cal/liter/min resulted in an increase in the per cent Scenedesmus from 7% at the 1-day period to 47% at the 3-day period. Extending the detention period to 4 and to 5 days, however, brought about a drop in per cent Scenedesmus to 28% and 22%, respectively. The same relationship held when the light energy input was advanced to 14.5 cal/liter/min. Except for a sharp increase upon lengthening the detention period from 1 to 2 days, no significant change in the ratio of Scenedesmus to Chlorella was brought about by lengthening the detention period, when the light energy input was maintained at 21.1 and 28.6 cal/liter/min.

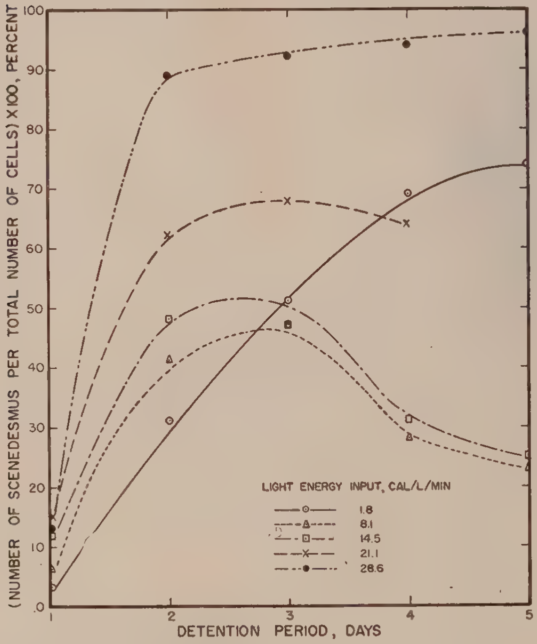

FIG. 6. The relation of various combinations of rates of light energy input and detention periods to the relative density of Scenedesmus.

The effect of detention period on the relative density of Scenedesmus and Chlorella was influenced by the periodicity, as is shown in Table IV.

TABLE IV. The effect of detention period upon relative numbers of Scenedesmus and Chlorella as modified by periodicity. The values given express the per cent of total population as Scenedesmus. The detention period was 2 days; concentration of CO_2, 2%, and light energy input, 28.6 cal/liter/min

Detention Period (days)	PERIODICITY (%)				
	40	50	60	70	80
1..........	13	26	66	70	90
2..........	15	50	82	91	93
3..........	17	84	93	95	94
4..........	20	88	92	94	93
5..........	25	92	91	96	96

At a detention period of one day, Scenedesmus never exceeded 25% of the algal population regardless of detention period. When the detention period was increased to 2 days, the range was from 26% of the algal cells at 40% periodicity to 92% at 80% periodicity. At a 5-day period, the range was from 90% of the algal population at a 40% periodicity to 96% at the 80% periodicity.

The combined effect of detention period and concentration of CO_2 upon the ratio of Scenedesmus to Chlorella is shown in Figure 7. Under the standard conditions of the experiments and

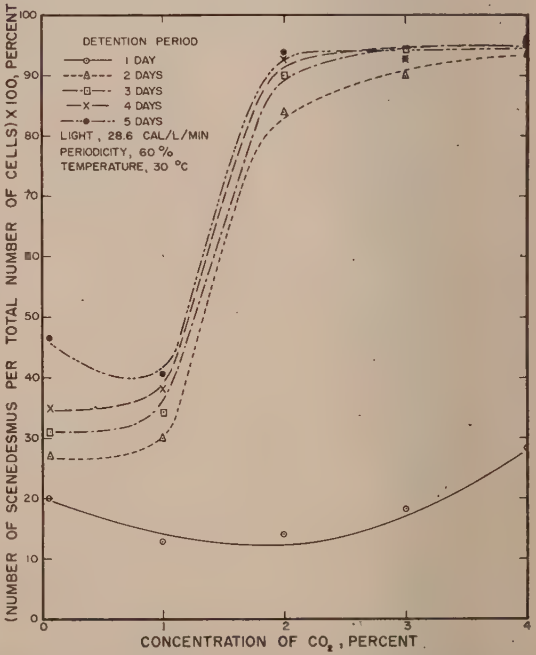

FIG. 7. The effect of detention period and concentration of CO_2 on the relative density of Scenedesmus.

at a 1-day period, Scenedesmus constituted less than 30% of the cells regardless of concentration of CO_2. Scenedesmus was also outnumbered by Chlorella at CO_2 concentrations of 0.03 and 1% at all detention periods, reaching a maximum of only 40% of the total culture at the 5-day period. With the exception of the 1-day period, Scenedesmus constituted from 90 to 95% of the culture at detention periods of 2 to 5 days and concentrations of CO_2 of 2 to 4%.

At CO_2 concentrations of 0.03 and 1%, Chlorella remained the dominant algal group regardless of periodicity; at higher concentrations and at all periodicities, Chlorella was superseded by Scenedesmus.

Discussion

Maximum concentrations of cells were reached in the experiment at a detention period of 3 days, and no further increase could be obtained by extending the period. The upper limit on cell number was probably a function of design of apparatus rather than of lack of nutrient or of intrinsic limitation in the cells themselves. An analysis of culture effluent showed appreciable residues of nitrogen and phosphorus at all of the detention periods. As the detention period was lengthened fewer cells were lost through dilution, and, consequently, the rate of production of new cells continued to exceed that of loss through dilution until the density of the culture became so great that cells located in strata under the surface of the culture received little, if any, light. Because of the mixing action of gas bubbling through the culture, however, cells were constantly being moved from positions in the surface layer to those within inner strata of the culture. Thus, the cells were exposed to alternating periods of light and dark. As the culture increased in density the time of exposure of each cell to light became increasingly short. Finally, a point was reached at which light available to the individual cells was so limited as to permit an average growth rate sufficient only to maintain the culture at the maximum density allowed by the design of the unit. Apparently, this density was reached with a 3-day detention period under the conditions of the experiments.

Except in cultures grown at a light energy input of 1.8 cal/liter/min, the number of cells was markedly increased when the CO_2 concentration was raised from 0.03% to 1%. Apparently the limitations placed upon photosynthetic activity at the low light energy input (1.8 cal/liter/min) were so great as to preclude any beneficial effect which might have resulted from an abundant supply of CO_2. Carbon dioxide was limiting when it was maintained at a concentration of 0.03% and the light energy input was greater than 1.8 cal/liter/min. This is shown by the fact that the maximum population density reached at any light energy input at 0.03% CO_2 was less than that at concentrations of 1% and higher. Light, in turn, became the limiting factor at concentrations of 1 and 2% CO_2, inasmuch as at these levels the number of cells increased with increase in light energy input, whereas the maximum attained at 1, 2, and 3% CO_2 was almost the same at each rate of light energy input. At a 4% concentration of CO_2 a factor other than light became limiting, because the size of the algal population attained at all levels of energy input dropped. Inasmuch as CO_2 concentration was the only factor changed, the decline must have been due to an inhibiting effect exerted on algal growth by an excess of CO_2. The inhibitory effects of excess CO_2 on photosynthetic activity have been discussed at length by Rabinowitch (1945, 1951, and 1956).

The results of the experiments showed that CO_2 concentration was a decisive factor in determining the relative incidence of Chlorella and Scenedesmus, in that at the lower concentrations (0.03 and 1%) Chlorella constituted the major portion of the algal population regardless of variations in temperature, light energy input, periodicity, and detention period within the limits prevailing during the study. On the other hand, Scenedesmus usually were more numerous than Chlorella at CO_2 concentrations greater than 1%. The higher concentrations may have been inhibitory for Chlorella, and perhaps, more approximate to the optimum for Scenedesmus. Either possibility would be to the advantage of Scenedesmus.

The ability of Chlorella to outnumber Scenedesmus at a detention period of 1 day probably indicates that the former has a shorter generation time than the latter. This competitive advantage became less important when the detention period was longer than 1 day, and consequently, the dominance of the one or the other was then determined by other factors, either individually or combined.

There was no specific level at which light energy input or temperature determined the dominance of one or the other organism. Low or high levels of either factor could be compensated for by appropriately varying the remainder of the environmental complex. Thus, certain combinations of conditions resulted in the dominance of one or the other of the organisms. For example, Scenedesmus always constituted the dominant algal group when the concentration of CO_2 was 2% or more; temperature, 20° to 40°C inclusively; light energy input 14.5 cal/liter/min or more; periodicity, greater than 50%; and detention period, 3 days or longer. As far as extent of dominance of Scenedesmus was concerned, the nature of the combinations of all of the factors studied exerted the final effect. In general, long detention periods, high rates of light energy input, long periodicities, temperatures less than 40°C, and concentrations of CO_2 greater than 1%, all helped to increase the ratio of Scenedesmus to Chlorella. Conversely, short detention periods, low rates of light energy input, short periodicities, CO_2 concentrations of 1% or less, resulted in high percentages of Chlorella.

In considering the effect of light as a variable, it should be remembered that periodicity and light energy input both determine the amount of light energy available. Therefore, a high rate of light energy may compensate for short periodicities, and vice versa. Periodicity, however, can also exert an independent effect because it limits the generation time of the algal cells and also determines the extent of the beneficial as well as of the inhibitory effects of either the light or of the dark period.

Results of these studies may be used to explain the seasonal shift in algal population in outdoor pilot plant high-rate ponds reported by Oswald and his colleagues (1958). Their report states that, from the end of November until the first part of March or April, *Chlorella spp* constitute the dominant algal group; however, as spring and summer progress, Chorella disappear and are replaced by Scenedesmus. But as autumn gives way to winter, Scenedesmus again become increasingly scarce, while Chlorella increase in number. Because the same detention period is usually followed throughout the year in operating the ponds, the reduction in hours of daylight during the winter months amounts, in effect, to a reduction in growing time for the algae. The rate of light energy input also declines with the coming of winter because of the angle of incidence of the sun's rays. Moreover, at this time of the year, the CO_2 concentration of the pond is lower, because bacterial activity is retarded by the prevailing low temperatures. These 3 factors, short growing time, reduced light energy input, and lower concentration of CO_2, as the present study demonstrates, give a competitive advantage to Chlorella during the winter months. Conversely, as summer approaches, the time of daylight and detention period is extended, light energy input is increased, and more CO_2 is produced in the ponds. All of these conditions favor the growth of Scenedesmus over that of Chlorella, and hence, Scenedesmus forms the predominant algal group during the summer.

The experiments on the effect of various environmental factors on the efficiency of the culture demonstrated that the efficiency attained by the culture was determined by the environmental complex, and not by the predominant type of organisms. For example, conditions favoring maximum efficiency in this study were a 2-day detention period, 30°C temperature, 60% periodicity, and a concentration of CO_2 of either 1 or 2%. As has been stated previously, when the concentration of CO_2 was maintained at 1% Chlorella always constituted the predominant organism. On the other hand, when the concentration of CO_2 was increased to 2%, and conditions were those listed above, Scenedemus were predominant. An analysis of the data listed in Tables I and II offers additional evidence of the extremely limited influence of algal type, Scenedesmus or Chlorella, on efficiency in the present study. A comparison of the efficiencies obtained at 1 and 2% CO_2 at each of the periodicities and light energy input rates shows that the variation in efficiency with change in the two latter factors was almost identical at the two concentrations of CO_2, despite the fact that Chlorella formed the dominant group at lower, and Scenedesmus at higher concentrations of the gas.

The decrease in over-all efficiency of the cultures with the extension of the detention period was a function of cell age and of an insufficient supply of light to the individual cells which, in turn, was due to the increasing density of the culture. As the detention period is lengthened in continuous cultures, the average cell remains for a longer period of time in the culture, and thus the average age of the individual cell may be extended. It is true that the cells could continue to divide, and hence the individual cell need be no older at long than at short detention periods. But because nutrients and light become limiting as the number of cells increases, conditions are no longer favorable for growth and reproduction; therefore, the average cell divides with less frequency. As the cells age, or as conditions become less favorable for reproduction, over-all efficiency of the culture decreases.

SUMMARY

A study was made of the ecology of a biotic community consisting of various bacterial and protozoan groups and of the algae, *Chlorella spp* and *Scenedesmus spp*. It included an evaluation of the effects of detention period, CO_2 concentra-

tion, light energy input, periodicity, and temperature upon the photosynthetic efficiency, population number, and composition of the biotic community, when functioning as a continuous culture.

At temperatures of 25°, 30° and 35°C, photosynthetic efficiency declined when the detention period was extended from 1 day to 5 days, whereas at 20°C, it increased as the detention period was lengthened from 1 to 3 days, and declined at longer periods. Highest efficiencies were obtained at 40°C, when the detention period was maintained at 5 days, and lowest, at 1 day. Optimum concentations of CO_2 were within the range 1 to 3%. Some inhibitory effects were noted at conconcentrations of 4%. Lowest efficiencies were obtained at a light energy input of 1.8 cal/liter/min, and highest at 8.1 cal/liter/min. Efficiency declined as the light energy input was increased beyond 8.1 cal/liter/min. The effect of periodicity on efficiency was only slight.

In general, cell concentration was highest at CO_2 concentrations of 1 to 3%. The effect of concentration of CO_2 was markedly influenced by light energy input and less so by detention period. Cell concentration increased in porportion to increase in light energy input. Lengthening the detention period from 1 to 3 days resulted in a linear increase in cell concentration; however, the population density remained relatively stationary with additional extensions of detention period.

Scenedesmus formed the dominant algal group when combinations of environmental factors included detention periods of 3 days or longer, CO_2 concentrations of 2% or more, light energy input rates of 14.5 cal/min/ or more, and periodicities of 60% or longer. On the other hand, Chlorella outnumbered Scenedesmus at 1-day detention periods and at concentrations of CO_2 of 1% or less. In general, with respect to relative numbers, Chlorella was favored by short detention periods, low light intensities, short periodicities, and low concentrations of CO_2.

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COMPARISON OF VEGETATION OF KANSAS-NEBRASKA DRIFT-LOESS HILLS AND LOESS PLAINS

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The western edge of True Prairie gives way very gradually on the Loess Plains south of the Platte River to Mixed Prairie of the Great Plains. North of the Platte a similar transition occurs in the valleys and on the slopes of the Loess Hills. But in northern Kansas the True Prairie of the Kansas-Nebraska Drift-Loess Hills is definitely separated by the Flint Hills Region from its western edge on the Kansas-Nebraska Loess Plains. In this study the vegetation, soils, and other environmental factors of the two areas are described and compared.

Names of grasses are according to Hitchcock and Chase (1950) revised Manual of Grasses of the United States. Other scientific names follow Gleason's (1952) New Britton and Brown Illustrated Flora.

AREA OF STUDY

These studies were made in northeastern Kansas and in the eastern portion of north-central Kansas (Fig. 1). They were mostly in the two tiers of counties adjacent to the Kansas-Nebraska state line but also included the adjoining tier of

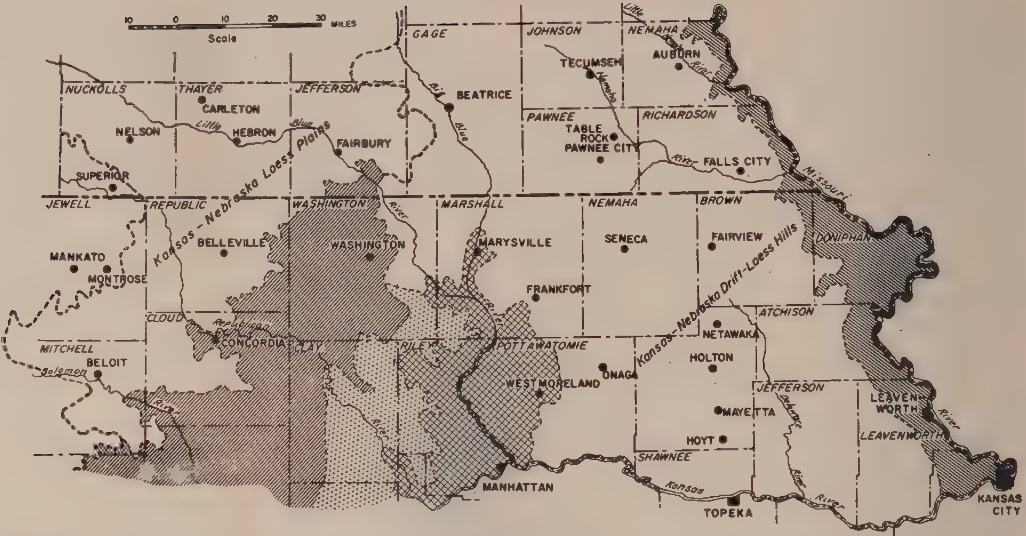
10 0 10 20 30 MILES
Scale
GAGE
JOHNSON
NEMAHA
Little
TECUMSEH
AUBURN
NUCKOLLS
THAYER
JEFFERSON
BEATRICE
CARLETON
PAWNEE
RICHARDSON
NELSON
Little Blue
HEBRON
FAIRBURY
TABLE ROCK
PAWNEE CITY
FALLS CITY
SUPERIOR
Missouri
JEWELL
REPUBLIC
WASHINGTON
MARSHALL
NEMAHA
BROWN
Kansas-Nebraska Loess Plains
BELLEVILLE
WASHINGTON
MARYSVILLE
SENECA
FAIRVIEW
DONIPHAN
MANKATO
MONTROSE
FRANKFORT
Kansas-Nebraska Drift-Loess Hills
CLOUD
ATCHISON
NETAWAKA
MITCHELL
CONCORDIA
CLAY
RILEY
POTTAWATOMIE
HOLTON
BELOIT
Solomon
WESTMORELAND
ONAGA
JEFFERSON
LEAVENWORTH
MAYETTA
LEAVENWORTH
HOYT
SHAWNEE
MANHATTAN
Kansas River
TOPEKA
KANSAS CITY

Fig. 1. Map of the Kansas-Nebraska Drift-Loess Hills and Loess Plains. The Flint Hills and other areas separating them, and the Loess Hills Region along the Missouri River are also shown. The heavy broken line separates Kansas (southward) from Nebraska.

counties in southern Nebraska. Most of the work was done in 1929-32 before the great drought of 1933-40, but the results have been confirmed by further examinations in 1952-53 and 1959. The eastern area is the Kansas-Nebraska Drift-Loess Hills, a large territory which lies north of the Kansas River (Fig. 1). The western area is the Kansas-Nebraska Loess Plains, about 100 miles westward. They are separated in part by the Flint Hills (cross-hatch) and partly by the Shale-Sandstone Section (parallel lines) of the Central Kansas Rolling Plains Region.

The Flint Hills Region occupies the western half of the eastern third of Kansas. It extends southward from near the Nebraska state line entirely across the state. The general width is about 60 mi, but it narrows north of the Kansas River to about 30 mi. The region was so called from the underlying cherty or flinty limestone. Here the soils have developed on Pennsylvanian limestone. From the excellent cover of bluestem grasses it is often designated as the Bluestem Hills.

In the Shale-Sandstone Section which lies westward, in northern Kansas, there are extensive areas where sandstone caps the hills and rough broken lands; the eroded lower parts are chiefly clays and shales. In this area the soils have developed on Dakota Sandstone and Permian Shales. Deposits of pale yellow and brownish loess are on the nearly level to gently sloping, narrow divides in the northern third of the area (*cf.* Fly 1946). The entire area was formerly covered with bluestem prairie. This, however, was not of the same high-yielding capacity as that of the Bluestem Hills. In the small, dotted part between the preceding areas the soil developed on loess overlying Permian Shales.

Thus, in Kansas, the Kansas-Nebraska Drift-Loess Hills are distinctly separated from the Kansas-Nebraska Loess Plains. Northward, however, the Drift-Loess Hills Region, which has been glaciated and also deeply covered with loess, merges gradually into the non-glaciated Loess Plains. True prairie as distinguished from the drier Mixed Prairie just westward, but not shown on the map, occupied the whole of the mapped area (Fig. 1). The Loess Plains section occurs throughout in the Chernozem rather than in the Brunizem (Prairie) Soil Zone.

The northern boundary of Kansas is 40°N latitude. The parallel of 39° is only a few miles south of Topeka. The meridian of 96° west longitude is slightly east of Seneca, and that of 98° is a few miles east of Superior and Montrose (Fig. 1). Altitude in the Drift-Loess Hills ranges from approximately 1,300 ft (Frankfort, Seneca and Onaga) to about 1,000 ft near Topeka. At Table Rock it is 1,100 ft. The Loess Plains are somewhat higher, 1,600 to 1,500 ft.

CLIMATE

The climate is characterized by moderately long, cold winters and a growing season of about 165-

180 days, late April to early October, without killing frost. Normal summer temperatures are about 75° F, but the maximum day temperatures may reach 100°F or more. Mean annual precipitation at the Loess Plains stations, before the great drought in 1933-1940, was 25 in. at Montrose and 27 in. at Hebron. Over the Drift-Loess Hills it varied mostly from 28 to 33 in., but reached a maximum of 37 in. in the extreme southeast. Westward from the Missouri River along the Kansas-Nebraska border rainfall decreases at an average rate of 1 in. per 15 mi. to Superior, Nebraska. Seasonal distribution is very favorable to the growth of grasses; 75 to 79% usually occurs between April 1 and September 30. Winds, although often high, are less frequent and of lower velocities in the eastern prairies than on the Loess Plains. Humidity is often 10-15% higher east than west of the Flint Hills, and evaporation is much greater westward. According to Thornthwaite's (1931) P-E index, precipitation effectiveness is much greater in the Drift-Loess Hills. Here it ranges from 56 to 64, but in the western area from 44 to 48.

The Kansas-Nebraska
Drift-Loess Hills

Southeastern Nebraska and a large area in Kansas north of the Kansas River and east of the Flint Hills is known as the Drift-Loess Hills (Fig. 1). The soils, previously developed over bedrock of limestone, flint rock, sandstone and limey and clayey shales, were covered by debris brought down by the great ice sheets, the Kansan glacier. In the southern part, however, the till sheet was relatively thin. Before the glacial drift was capped by loess, erosion had removed and resorted considerable amounts of this material. The mantle of Peorian Loess and later deposits is thickest (100 ft in places) along the bluffs of the Missouri River (Frye and Leonard 1951). It decreases in depth westward, for example, to about 6 ft, 13 mi. southwestward in Brown County (Hanna and Bidwell 1955). These investigators state, "There seems to be fairly general agreement that in the Mississippi Valley, including the Missouri River, loess was deposited by wind and that its source was the flood plains of the Pleistocene rivers" (Leonard and Frye 1954). The Loess Hills Region is a strip 6 to 15 mi. wide along the Missouri River with a thick covering of loess derived from the Missouri flood plain. Westward the Platte and other Pleistocene Rivers may have furnished the thinner layer of wind-blown loess.

The topography, soils, and vegetation of the eastern and western areas will be considered separately.

Topography and Soils

The Kansas-Nebraska Drift-Loess Hills Region generally "has narrow, gently rolling divides, with long, moderate to moderately steep slopes broken by rough, stony land, and bedrock outcrops just above the smooth broad valleys. The southern part is much more rolling and is hilly to rough and broken in places" (Fly 1946). Drainage is southward except in Richardson County, Nebraska, in the northern part of Nemaha and Brown counties, Kansas, and along the eastern edge where the streams flow to the Missouri River. Winds have deposited fine silts and clays over much of the region, especially the northern half.

Chief soil series are Grundy, Crete, Pawnee, Burchard and Shelby. The first two are silty clay loam soils derived from loessial parent materials and occur on the nearly level divides. Pawnee, Burchard and Shelby soils, derived from glacial till, occur mostly on undulating to rolling land. In general, the bedrock usually lies 5 to 25 ft or more below the soil surface. All the soils are very dark-grayish or dark-grayish brown. Permeability varies from moderate (Burchard) to very slow in Crete and Pawnee soils. Both soil and subsoil have high water-holding capacity (*cf.* Bidwell 1956). There is no distinct layer of lime accumulation although the lime is not completely leached from the subsoils. Under grass they are nearly neutral to somewhat acid in reaction. Productivity is moderately high. Dominant crops are corn, small grains, alfalfa and sweet clover, and grasses. "Next to the Loess Hills region, this is the state's most productive area" (Fly 1946).

The Prairie Grasses

It has been ascertained after many years of study that the vegetation of True Prairie on uplands consists of three major types or communities. Dominant grasses, after which the communities are named, are little bluestem (*Andropogon scoparius*), needlegrass (*Stipa spartea*) and prairie dropseed (*Sporobolus heterolepis*). Several other mid grasses of importance occur in variable abundance in each of these types, but none forms a community of its own.

Prairie of the more moist and wet lowlands is also composed of three communities, each dominated by tall grasses. The most extensive is that of big bluestem (*Andropogon gerardi*). A second community occurs in soils usually of higher water content than that of the preceding. It is composed mostly of switchgrass (*Panicum virgatum*) but also of Canada wild-rye (*Elymus canadensis*). Prairie cordgrass (*Spartina pectinata*) forms a third tall-grass community. It originally occurred in nearly pure stands over hundreds of square miles of first bottom lands along the Missouri and other great rivers and their tributaries.

Mid grasses of uplands can not compete successfully with tall grasses on lowlands because of the dense shade produced by them. Conversely, upland soils are usually not sufficiently moist to promote good development of tall grasses, especially in competition with mid grasses. Of course there is much intermixing of some tall grasses on lower hillsides, or even on level, poorly drained hilltops. Conversely, mid grasses are often scattered sparingly over lowlands. General descriptions of the prairie communities, including their composition and structure, have been given by Weaver and Fitzpatrick (1934). A more succinct statement may be found in North American Prairie (Weaver 1954).

In the area of this study little and big bluestem were by far the most abundant grasses. Prairie dropseed and needlegrass occurred only locally. The prairie cordgrass and switchgrass—wild-rye communities were of common occurrence, but they will be considered only incidentally, since those along the Missouri River and its tributaries in True Prairie have recently been fully described (Weaver 1960).

The characteristic habits of growth, the relations of the roots to tops, and certain other characteristics of the several community dominants are shown in Figures 2 and 3. The tall grasses of the lowland types are sod formers as a result of their rhizome development. The great foliage height of big bluestem, about 3.5 ft, is exceeded by that of switchgrass, and both are surpassed by prairie cordgrass. Flower stalks of switchgrass may attain heights of 6-7 ft and those of big bluestem and prairie cordgrass 6-10 ft. In the figures only the amount of tops that occurred in a strip of soil 1 in. in width is shown. Likewise the average number of roots is from an inch-wide column of soil. These data were ascertained for each foot in depth from perpendicular walls of trenches and from monoliths taken from many different soils. Relative width of the main roots of the several grasses is also shown. Only enough detail has been added to indicate the branching habits.

In upland, True Prairie grasses the bunch habit of growth prevails. The average spacing of bunches, about 1-1.5 ft apart, is shown. The largest roots have only about one-third the diameter of those of big bluestem. Note that the soil beneath the crown and on all sides of it to a

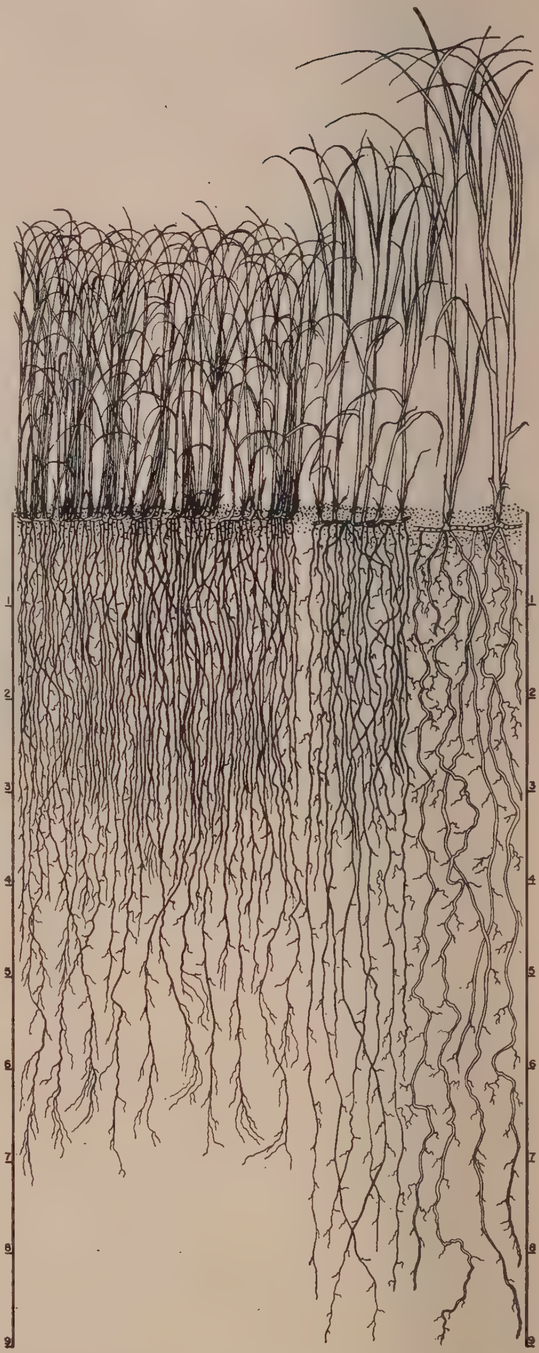

FIG. 2. Characteristic development of tops and roots of big bluestem (*Andropogon gerardi*) (left), switchgrass (*Panicum virgatum*), and prairie cordgrass (*Spartina pectinata*) (right). When flower stalks are fully developed and flowering occurs, heights of 6 to 10 feet are attained.

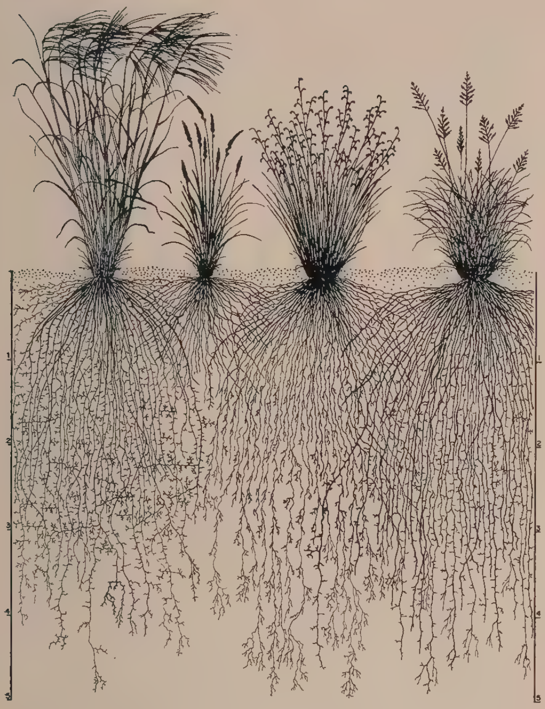

FIG. 3. Characteristic development of tops and roots of four bunch grasses as they occur in the several upland communities. From left to right they are needlegrass (*Stipa spartea*), Junegrass (*Koeleria cristata*), little bluestem (*Andropogon scoparius*) and prairie dropseed (*Sporobolus heterolepis*). Note that the tops are only about half as high as the roots are deep.

distance of 12-16 in. is threaded with dense mats of roots to a depth of 4-5 ft. A thorough study of the underground development in natural grassland communities was summarized by the writer in 1958, from which the following paragraphs are taken.

The sod-forming tall grasses of lowland communities of true prairie are of the greatest height (5-10 ft), have the greatest leaf surface, and produce the largest amount of forage. Their roots are coarsest, least well branched, but deepest. They are about as deep (7-10 ft) as the stems are tall. Roots do not spread widely just below the soil surface. All of the dominants, except *Elymus canadensis,* are warm-season grasses that grow all summer and flower late.

Upland mid grasses nearly all grow in bunches. They are of intermediate height (2-3.5 ft), leaf surface, and amount of forage production. Roots are moderately fine, well branched, and moderately deep. They are about twice as deep (4-5.5 ft) as the stems are tall. They are fairly well spread and moderately dense just beneath the soil surface. Grasses from lowland, when growing in upland, are reduced in size and weight. The roots are somewhat finer and more branched but penetrate less deeply. There are several cool-season grasses on uplands which flower early but most are warm-season species, flowering late after a long season for growth.

Prairies Near Topeka

Two large prairies, totaling more than 300 acres, were examined. One was about 11 mi. north of Topeka and the other about 2 mi. north of Hoyt (Fig. 1). The hills varied from 50 to more than 100 ft in height above the valleys. In both prairies little bluestem dominated on the hilltops and upper and mid slopes, but on lower slopes as well as on gently sloping land in the valley big bluestem was the chief grass.

On the hilltops where the drift soil overlying the limestone was shallow the cover of vegetation was variable. Little bluestem and prairie dropseed in various mixtures often dominated locally. More usually little bluestem, in the bunch form, prevailed and often alone composed 80-90% of the vegetation. Height of foliage was only 9-11 in. in midsummer and in places the foliage cover did not exceed 50%. Big bluestem was present in small tufts or bunches only to the extent of about 5%.

Over the hilltops and ridges in general, little bluestem was the most abundant grass, usually about 70% in amount and in midsummer 18-24 in. high. In places with more moist soil big bluestem increased to 15-40% locally, but over the hilltops as a whole it averaged about 5%. Here it occurred mostly in the bunch form. Switchgrass grew as scattered tufts more or less throughout but rarely, except very locally, exceeded 5% in abundance. Indian grass (*Sorghastrum nutans*) was even less abundant. As a result of marked variations in soil depth and water content, vegetation appeared very uneven in both height-growth and density of stand. Eastern gamagrass (*Tripsacum dactyloides*) was found where seepage occurred; Canada wild-rye was sparsely represented.

The hillsides were clothed with a mixture of little and big bluestem. The first was dominant on higher ground, but big bluestem increased to 50% or more on the lower slopes and the level base. Here it prevailed in the sod type, sometimes forming as much as 60-80% of the vegetation. This distribution was readily apparent but was verified by a large number of square-meter quadrats (Table I).

The percentages are not based upon foliage cover (the area occupied by the spreading tops

TABLE I. Percentage composition of vegetation in square meter quadrats from upper slope to the base of a long, rather gentle south slope near Topeka; July 1930

Species	Upper slope					Mid slope					Lower slope					Level base				
Little bluestem	68	65	40	81	69	70	66	52	75	47	12	15	18	15	8	13	16	8	5	12
Big bluestem	7	10	9	10	8	20	16	30	20	13	67	63	60	65	71	76	80	84	89	77
Prairie dropseed	14	15	50	—	—	9	5	6	—	—	—	—	—	—	2	—	—	—	—	—
Switchgrass	—	—	—	2	8	—	—	10	4	5	2	—	5	6	—	8	2	—	—	11
Indian grass	1	—	—	2	—	1	6	—	1	3	—	8	4	3	6	2	1	5	—	0
Foliage cover %	55	50	65	50	60	70	65	75	80	80	100	90	100	95	100	95	100	100	100	100
Basal area %	15	14	10	13	15	14	11	12	18	10	13	13	13	12	14	13	15	16	13	15

of the plants in the several layers of vegetation above the soil surface). This varies with the progress of the season and from dry to wet years. In July and later it was usually 75-100%. The basal or ground cover is the actual area occupied by the stems, mats, or tufts of plants about an inch above the soil surface. It is fairly stable and varies but little from month to month or year to year. The part of the total basal cover (considered as unity) composed by each species is that shown in Table I. The remaining basal cover was that of other vegetation. It should be noted that the two bluestems usually composed fully 80% of the vegetation. The nature of these warm-season, perennial, dominant grasses has previously been fully described (Weaver and Fitzpatrick 1932).

Where seepage occurred on hillsides both eastern gamagrass and switchgrass were common. Even on lowlands little bluestem was usually second in abundance. In places switchgrass had an abundance of 10% but Indian grass seldom exceeded 5%. In the wet soil of valley floors big bluestem was replaced by prairie cordgrass and eastern gamagrass. In both prairies side-oats grama (*Bouteloua curtipendula*) was intermixed throughout the bluestems but in very small amounts. Junegrass (*Koeleria cristata*) was common, except among the tall grasses on low ground, and often abundant where other vegetation was not dense. Needlegrass was rarely found. The wide range of switchgrass over much of the area was quite different from the restricted one in prairies on the deep loess soil of southwestern Iowa (Weaver 1958b).

Onaga Prairies

Excellent, annually mowed prairies are plentiful near Onaga and southward to the Kansas River. From 75-90% of the land is used for grazing because of the rock-filled soil, in places glacial boulders, elsewhere limestone or sandstone.

Along an intermittent stream in the valley at the foot of the hills, dense stands of prairie cordgrass were found. This coarse grass attained a foliage height of 6.5 ft. It alternated with patches of eastern gamagrass of similar stature and even coarser foliage. In places the two intermingled. A characteristic understory, especially to cordgrass, was composed of scarlet strawberry (*Fragaria virginiana*), yellow sheep sorrel (*Oxalis stricta*), stiff marsh bedstraw (*Galium tinctorium*), American germander (*Teucrium canadense*) and fringed loosestrife (*Steironema ciliatum*). Tall forbs, such as water hemlock (*Cicuta maculata*), saw-tooth sunflower (*Helianthus grosseserratus*), entire-leaved rosinweed (*Silphium integrifolium*) and tall goldenrod (*Solidago altissima*) also were common but not abundant. Indigo bush (*Amorpha fruticosa*), rough-leaved dogwood (*Cornus drummondi*) and coralberry (*Symphoricarpos orbiculatus*) occurred in ravines. In a few places little bluestem extended downward from the upland and gave way abruptly to prairie cordgrass or eastern gamagrass. But usually there was a wide transitional belt on lower slopes where big bluestem was dominant and little bluestem from the mid slopes intermingled with it in moderate amounts.

On lower slopes there was a wonderfully developed stand of big bluestem. Its midsummer foliage height was 28-34 in. Intermixed in small amounts were tall plants of side-oats grama and larger proportions of Canada wild-rye and switchgrass. Indian grass, with a height similar to that of big bluestem, composed in places as much as 5-8% of the cover. Only small amounts of Kentucky bluegrass (*Poa pratensis*) were found. The total foliage cover was 90-100%.

On the mid slopes vegetation varied from a dense cover of grasses, mostly little bluestem of the sod-mat type, to places where the grasses were intermixed with a great abundance of forbs. Nearly always little bluestem was 18-22 in. tall by midsummer, and it frequently grew in nearly pure stands. It formed the bulk of the vegetation over the mid and upper slopes; the foliage cover was 80-90%. Big bluestem produced good stands in places but it was mostly mixed with little bluestem, in amounts of only 1-15%. It exceeded the dominant in height by about 6 in. Halfway down some north-facing slopes the two bluestems were of about equal abundance, but little bluestem often composed a considerable part of the cover on drier, lower slopes.

On hill crests where the rock sometimes outcropped, the cover of grass was thinner, but forbs were of more than usual abundance. This resulted in an uneven, ragged appearance of the prairie. But often there was as much big bluestem, switchgrass, and side-oats grama here as in apparently deeper soil on the hilltops. Even on mid slopes where rock outcropped there was a similar open cover and some bare soil occurred.

Other grasses generally varied greatly in amount over the prairies, but none attained the rank of the bluestems. Indian grass usually formed 1-5% of the cover but it had a very irregular distribution, and on some ridges it increased to 15-25%. Kentucky bluegrass varied in amount from 0 to 3%. Prairie dropseed occurred sparingly in a few places, some on upper slopes, some on low ground. Scattered plants of Canada wildrye and switchgrass were found throughout. Like eastern gamagrass they were most abundant about hillside seeps. Side-oats grama ranged throughout but was of most frequent occurrence, 1-5%, on upland. Needlegrass was infrequent; scattered plants grew on the driest ridges or in washes on lowland. Junegrass was often absent; it rarely exceeded 5% anywhere. Low-growing panic grasses such as *Panicum scribnerianum* and *P. wilcoxianum,* and also penn sedge (*Carex pennsylvanica*) were never very abundant.

In many ungrazed prairies both switchgrass and Indian grass were often scattered throughout. In midsummer when the little bluestem foliage was 20 in. high on upland, Indian grass usually was 8 in. and switchgrass often 16 in. taller, although neither was as tall here as on lowland. Each was represented by a few widely scattered stems, by bunches, or by small patches of a continuous sod. Since the leaves are more erect than those of the bluestem, this results in an uneven or ragged appearance, which is quite different from the more uniform one in more northerly prairies.

These every extensive bluestem prairies were from June to October a land of waving grasses bedecked by an abundance of varicolored flowers above, within and beneath the foliage of the grasses. The forb population will be considered separately following the distribution of the grasses in other samples of prairie.

Grassland Near Mayetta

A prairie one sq. mi. in area lies about 20 mi. north of Topeka and 25 mi. southeast of Onaga. It differed from the preceding ones but little in the hilly topography but was quite different in composition of the vegetation. This resulted from annual burning over a long period of years. It was largely a little bluestem prairie, in which the foliage cover was 80-95%, the dominant often developing the sod-mat type rather than occurring in large, well spaced bunches. Even on the upper slopes and hilltops little bluestem had a midsummer stature of 12-14 in. It was usually accompanied by a marked development of switchgrass, which was far more abundant in this burned prairie than elsewhere. Switchgrass extended from its usual place in ravines and foot-slopes over all the hillsides and was also common on flat hilltops, thus assuming a distribution similar to that of big bluestem. Switchgrass was so widely scattered that it appeared in most of a series of quadrats, and to a considerable degree it replaced big bluestem.

The deep soil and its good water content were revealed by the presence of tall grasses, including Indian grass, on uplands where their foliage level was often 36 in. high. Big bluestem was dominant only on the lower slopes and in ravines, but it was present nearly everywhere, although not in its usual abundance. Over extensive areas switchgrass, 24-30 in. tall in midsummer, composed 50-80% of the vegetation. It did not occur in large bunches but had developed an open growth of sod similar to that found on low ground. The forage yield was 1.5 to 2 tons per acre. Eastern gamagrass grew in scattered bunches from lowland to the head of draws, and also occurred in wet depressions on hilltops.

Prairie dropseed was found in several local areas where very large bunches, sometimes 18 in. in diameter, were elevated a few inches above the general soil surface and filled with leafy shoots 15 in. high. Isolated tufts occurred elsewhere. There was almost no Junegrass or needlegrass. The almost complete absence of Kentucky bluegrass may be attributed to burning. Forbs were less abundant both in species and numbers than in the prairies previously described. Other burned prairies showed similar deviations in composition from those unmodified by annual burning.

Seneca Prairies

This large prairie 10-12 mi. southwest of Seneca occurred in several rather distinct sites. These were low, nearly level hilltops, ridges and crests of high hills, upper slopes, and mid slopes grading into nearly level lowland and then into swales. The soil seemed uniformly deeper than in the preceding prairies although a few glacial boulders occurred. Only about a third of the area could be classified as typical upland. Except on the ridges, portions of the hilltops, and on the steepest slopes, big bluestem was dominant. In the swales it was intermixed with moderate amounts of switchgrass and Canada wild-rye, and in the wetter places with prairie cordgrass. Thus, it dominated over two-thirds of this prairie area.

On the nearly level hilltops little bluestem and big bluestem with 5% or more Indian grass were intermixed. Bunches of little bluestem with occasional plants or small patches of prairie dropseed composed about two-thirds of the cover. Where increased runoff occurred, big bluestem decreased in amount and only on some of the low, flat hilltops did it rather constantly exceed little bluestem in abundance.

On hill crests or ridges little bluestem, supplemented by 10-20% of prairie dropseed, held possession with large, well developed bunches. Here this dominant was about 15 in. tall. The 5-10% intermixed big bluestem exceeded this midsummer height by 6 in. Low-growing Scribner's and Wilcox' panic grasses were common in the understory.

The little bluestem type on south and southwest slopes did not extend so far downward as in the preceding prairies and the greater abundance of big bluestem became apparent higher up the hillsides. Indeed, on north slopes of low hills it extended almost to the hilltops and little bluestem was reduced to 35% or less. Foliage of big bluestem and Indian grass in midsummer reached a height of 20-24 in. on upland but 36 in. on low ground.

Others grasses were of little importance. Blue grass varied in amount from 1 to 10%. Side-oats grama and Junegrass were sparse, and needlegrass was almost rare. Canada wild-rye occurred sparingly except in ravines. Several small clumps of coralberry occurred, smooth sumac (*Rhus glabra*) and roughleaf dogwood grew sparingly in ravines, and a small thicket of wild plum (*Prunus americana*) was observed. There were a large number of forbs but only a few formed definite societies; most were of no great abundance or infrequent.

This prairie was more mesic than those near Topeka and Onaga, probably due to a deeper soil resulting from thicker deposits of glacial till and loess.

Netawaka and Fairview

The prairies at Netawaka and northward were increasingly nearer the Missouri River and apparently profited greatly from the deeper layer of loess. Over the low hills and on the higher ones as well, little bluestem was spread like a green carpet. The sod-mat type prevailed everywhere except when it alternated with local areas of prairie dropseed on upland. The density of stand and good height growth as well as an abundance of forbs reflected a productive, well watered soil. On more moist lower slopes little bluestem increased in height but shared its dominance with or was replaced by big bluestem, and to a less extent by Canada wild-rye, switchgrass and Indian grass. Here the general foliage level in midsummer was 2-3 ft; the vegetation was more dense and the yield greatly increased. The bordering ravines were occupied by eastern gamagrass, a nut rush (*Scleria triglomerata*), or prairie cordgrass. Data from numerous quadrats in this prairie are given in Table II.

TABLE II. Percentage composition of vegetation as determined by square meter quadrats near Netawaka, Kansas

Species	Upper south slope				Upper north slope				Lower slopes					
Little bluestem	92	91	70	74	65	63	42	71	45	—	—	—	—	—
Big bluestem	5	2	23	12	10	5	50	10	45	23	39	88	89	82
Switchgrass	—	1	1	5	—	30	—	—	—	75	60	—	8	2
Indian grass	—	1	1	—	—	—	—	3	3	—	—	—	—	1
Foliage cover %	65	75	85	80	80	90	85	90	100	95	95	100	100	100
Basal area %	12	15	11	14	13	17	13	14	17	15	15	19	16	15

Other grasses of 1-5% in amount occurred in a few of the quadrats. These were needlegrass, Junegrass, Kentucky bluegrass and low-growing panic grasses. In one quadrat on a ridge prairie dropseed composed 97% of the vegetation, and in a well-watered ravine other quadrats had 97 and 98% of prairie cordgrass and eastern gamagrass, respectively.

Very similar vegetation prevailed at Fairview and northward. That on the loess hills about Falls City and still farther northward at Auburn and Nebraska City, all just east of the isohyet of 32 in. rainfall, were even better developed. Thornber gave an excellent account of one of these large prairies in 1901, and all were carefully examined by Weaver and Fitzpatrick (1934). In most respects they were identical with those eastward in Bedford, Iowa, and closely similar and only slightly less mesic than those at Corning, Creston, and Guthrie Center in southwestern Iowa (Weaver 1958b). It should be pointed out that the loess deposits east of the Missouri River flood plain are deeper than those in Nebraska, probably because of the prevailing westerly winds. Broad, level hilltops in western Iowa still maintain a deep covering of loess where tall grasses thrive and are thus similar to those found on certain hilltops in northeastern Kansas and southeastern Nebraska.

Summary of Grasses

Little bluestem was the most abundant species. It was nearly always the chief dominant on ridges and upper and mid slopes. It occurred mostly as bunches in the southern part (Topeka, Hoyt, Onaga) but often in the sod-mat form northward. It was also usually dominant on flat hilltops where it composed about two-thirds of the vegetation. Here big bluestem was sometimes locally dominant; but generally over the area little bluestem composed 70 to 80% of the vegetation. Big bluestem was dominant over low, level land and lower slopes and in places (northward) even over mid slopes. Southward little bluestem was sometimes equally intermixed with it on mid and lower slopes; northward big bluestem often extended farther upland even to the crest on north-facing hillsides. It alone frequently composed 85% of the grasses in its type.

Prairie dropseed was found in most prairies, usually in nearly pure patches on upper slopes and ridges, sometimes in amounts of 10-20%. Scattered plants of needlegrass were found on the driest ridges or in lowland washes. Junegrass and Kentucky bluegrass were often present but nearly always in small amounts. Side-oats grama was most abundant (1 to 3%) in the little bluestem type, but it also occurred with the tall grasses. The low-growing *Panicum wilcoxianum* and *P. scribnerianum, Carex pennsylvanicum* and a few other sedges were usually present but not abundant in the understory.

Switchgrass ranged widely from pure stands in lowlands and ravines to bunches or sodded patches on hillsides. Where annual burning was practiced, it partly replaced big bluestem. Canada wild-rye was not at all abundant. Indian grass was widely distributed and intermixed with big bluestem in amounts ranging from 1 to 10 or more per cent. It profited as a result of disturbance by fire. On nearly level hilltops, with greatly decreased runoff and occasional depressions, all of the preceding mid and tall grasses were more or less intermixed. The two bluestems, with considerable amounts of switchgrass and Indian grass, were the most abundant. Prairie cordgrass thrived on wet land, as did also the tall, coarse eastern gamagrass. The latter also grew on hillsides or flat hilltops where seepage or depressions resulted in a sufficient water supply. A few other prairie grasses, such as *Agrostis hiemalis* and *Eragrostis spectabilis,* added little to the cover. *Juncus tenuis* and *Carex festucacea* were also present mostly in small amounts.

Prairie Forbs

Forbs are always present and often abundant in prairies. In places they are more conspicuous, although nearly always of less importance than the grasses. After five years of study in an area of 60,000 sq. mi. in prairie of six states, it was ascertained that 75 species of upland and 67 species of lowland forbs occurred in at least 10% of the 135 large prairies examined. In addition more than 200 other species were listed (Weaver and Fitzpatrick 1934).

In the present study the relative abundance and importance of each species of forb was studied and closely estimated. Its rank, whether high, intermediate or low, was ascertained only after examining a large part of each prairie. Size, abundance, duration, density of stand, and gregariousness were all considered. The general criterion for each species was the actual effect of the forb on the cover of grass and the proportion of the basal and foliage cover that it composed. Actually, the basal cover produced by forbs in true prairie averaged only 4.1% on upland and 3.6% on lowland. The foliage cover varied greatly; that of a single plant of a large coarse forb such as a rosin weed (*Silphium laciniatum*) sometimes occupied several square feet, but a hundred plants of flax (*Linum sulcatum*) only a few square inches. Because of their great differences in habits of growth, etc., forbs are considered separately from the grasses. An ecological description of each of the prairie forbs of high rank and most of those of intermediate rank has been given (Weaver and Fitzpatrick 1934).

The list of species forming societies of the first class in the prairies just described follows.

Amorpha canescens	Lead plant
Antennaria neglecta	Prairie cat's-foot
Aster ericoides	Many-flowered aster
Baptisia leucophaea	Large-bracted wild indigo
Ceanothus ovatus	Redroot
Erigeron strigosus	Daisy fleabane
Helianthus laetiflorus	Stiff sunflower
Lespedeza capitata	Round-headed bush clover
Petalostemum candidum	White prairie clover
Petalostemum purpureum	Purple prairie clover
Psoralea tenuiflora	Scurf pea
Schrankia nuttallii	Sensitive briar

In addition to 10 forbs the list also includes 2 shrubby species, *Amorpha canescens* and *Ceanothus ovatus.* Under annual mowing these behave as perennial forbs. Lead plant is perhaps the most conspicuous, most widely distributed, and most abundant of prairie plants except for certain grasses. Sensitive briar, although rarely occurring north of the Kansas-Nebraska border, is also a legume of considerable importance. All parts of this decumbent, widely spreading plant are thickly armed with hooked prickles.

The number of forbs of first rank in these prairies was very similar to that in many others. Over this grassland it usually varied between 7 and 15. Moreover, each of these species, except *Baptisia leucophaea,* was also of high rank in many other areas.

Species in the following list were of intermediate rank. Most were sufficiently abundant to form societies, others were merely scattered throughout.

Achillea millefolium	Milfoil
Aster azureus	Sky-blue aster
Aster drummondi	Drummond aster
Desmodium canadense	Showy tick trefoil
Desmodium illinoense	Illinois tick trefoil
Echinacea pallida	Pale purple coneflower
Euphorbia corollata	Flowering spurge
Fragaria virginiana	Scarlet strawberry
Kuhnia eupatorioides	False boneset
Liatris scariosa	Large button snakeroot
Linum sulcatum	Grooved flax
Rosa suffulta	Prairie rose
Rudbeckia hirta	Black-eyed Susan
Ruellia humilis	Fringe-leaf ruellia
Silphium integrifolium	Entire-leaved rosinweed
Silphium laciniatum	Compassplant
Solidago graminifolia	Bushy, fragrant goldenrod
Solidago missouriensis	Missouri goldenrod
Viola pedatifida	Prairie violet

Most of the preceding species formed societies of the first class in various other prairies, and also in individual prairies of this group. Only a few, *Linum sulcatum, Ruellia humilis* and *Aster drummondi* were consistently of lower rank. Conversely, a few species which were of highest rank in upland prairies elsewhere were found only among the species of low rank here. These are *Astragalus crassicarpus, Coreopsis palmata, Liatris punctata, Psoralea argophylla,* and *Solidago rigida.*

Species of low rank that were listed are given to complete the record; each is an integral part of the prairie. The list includes all species which were observed in the various prairies described.

Acerates angustifolia
Acerates hirtella
Acerates viridiflora
Allium canadense
Allium mutabile
Anemone cylindrica
Apocynum cannabinum
Artemisia ludoviciana
Asclepias sullivantii
Asclepias tuberosa
Asclepias verticillata
Asclepiodora viridis
Aster oblongifolius
Aster sericeus
Aster praealtus
Astragalus carolinianus
Astragalus crassicarpus
Baptisia leucantha
Boltonia asteroides
Cacalia tuberosa
Callirhoe alcaeoides
Cassia fasciculata
Circuta maculata
Cirsium undulatum
Commandra umbellata
Commelina virginica
Coreopsis palmata
Delphinium virescens
Desmanthus illinoensis
Echinacea pallida
Equisetum arvense
Equisetum laevigatum
Eryngium yuccifolium
Erythronium albidum
Galium aparina
Galium tinctorium
Gaura biennis
Gaura parviflora
Gentiana puberula
Glycyrrhiza lepidota
Helianthus grosseserratus
Helianthus maximiliani
Helianthus salicifolius
Helianthus tuberosus
Heliopsis helianthoides
Hieracium longipilum
Houstonia nigricans
Hypoxis hirsuta
Liatris punctata
Liatris pycnostachya
Liatris squarrosa
Lilium philadelphicum
Lithospermum canescens
Lithospermum caroliniense
Lithospermum incisum
Lobelia inflata
Lobelia spicata
Lomatium orientale
Lycopus americanus
Lygodesmia juncea
Lythrum alatum
Monarda fistulosa
Oenothera biennis
Oenothera serrulata
Oenothera speciosa
Onosmodium occidentale
Oxalis stricta
Oxalis violacea
Oxybaphus nyctagineus
Parosaela enneandra
Phlox pilosa
Physalis heterophylla
Physalis longifolia
Physalis virginiana
Polygala verticillata
Potentilla arguta
Psoralea argophylla
Psoralea esculenta
Ratibida columnifera
Ratibida pinnata
Rhus radicans
Salvia pitcheri
Scutellaria leonardi
Silene anterrhina
Sisyrinchium angustifolium
Solidago altissima
Solidago canadensis
Solidago rigida
Solidago speciosa
Specularia perfoliata
Spiranthes cernua
Steironema ciliatum
Strophostyles helvola
Teucrium canadense
Thalictrum dasycarpum
Tradescantia bracteata
Verbena hastata
Vernonia baldwini
Vernonia fasciculata
Vicia americana
Viola papilionacea
Zizia aurea

The number of forbs in prairie is very large. Although their abundance is highly variable they compose perhaps 5-15% of the vegetation. They are nearly always most abundant in prairies with good precipitation and, as will be shown, less abundant in drier ones. Competition for light between grasses and forbs is often great and readily observed. There is also much competition in the soil for water and nutrients. The roots of accompanying forbs have not been shown in figures 2 and 3, but three general patterns of root systems of the perennial forbs are found among the grasses.

A dozen or more species, such as pale purple coneflower and silver-leaf psoralea (*Psoralea argophylla*), have taproots or several main roots which produce relatively few or no branches, but which penetrate deeply and often far below the roots of the grass. Another group, including false boneset, prairie clovers, ground plum (*Astragalus crassicarpus*) and blazing star (*Liatris punctata*), has taproots with widely spreading branches which also pentrate deeply. Plants in this group probably absorb mostly from depths greater than those most thickly occupied by the roots of grasses. The type of forb that competes most severely with the roots of grasses includes plants such as many-flowered aster, stiff sunflower, Missouri goldenrod, and Baldwin's iron weed (*Vernonia baldwini*). They spread by means of rhizomes and root offshoots or develop corms with numerous main roots of about equal size. Roots of species in this large group often compete severely with those of grasses, but also extend quite beyond the main depth (*cf.* Weaver 1958a).

The beauty of the grassland is greatly enhanced by the presence and abundance of this great variety of forbs. Furthermore they add to its value for grazing and hay. On some hillsides the purple prairie clover grows so thickly that when in bloom its rose-purple color overshadows the green of the grasses. Redroot, where abundant, may greatly suppress the grasses; its profusion of white flowers lightens the prairie. Societies of black-eyed Susan, goldenrods and sunflower produce patches of yellow and gold. So numerous are the species and so variable are their groupings that each prairie seems different from the others.

Kansas-Nebraska Loess Plains

The western area is a part of the nearly level to gently rolling plain where the bedrock has been covered to a considerable depth by loess and loess-like materials. This area consists primarily of broad smooth divides with rolling land adjacent to narrow valleys draining into the Republican and Solomon Rivers in Kansas and the Republican and Blue Rivers in Nebraska. Some shallow and broken or stony lands occur adjacent to drainage ways. The bedrock consists primarily of heavy shales and limestone, but only a small percentage of the soils, chiefly on the steeper slopes, are developed directly on the bedrock (*cf.* Fly 1946). The area is characterized by the dominance of heavy clay or claypan-like soils on the smooth divides and by bedrock nearly completely covered by loess.

Silty clay loam soils prevail. They are Crete, Hastings and Nuckolls. The heavier Crete soils tend to occur on nearly level land. The first two soils are very dark grayish-brown. They developed from Peorian loess and occur on nearly level to rolling relief. Nuckolls soil is dark brown or reddish-brown. It has developed in an older, reddish-brown (Loveland) loess, which outcrops on the slopes. Minimum depth to bedrock is usually 4-5 ft and greater depths vary from 12-25 ft or more. The soils are relatively fertile and have good water-holding capacity but the subsoils vary in permeability from moderate in Nuckolls, to moderately slow in Hastings, to very slow in Crete. This large area lies in the eastern portion of the Chernozem soil zone and the layer of lime accumulation is usually at a depth of 5-6 ft. Wheat and corn are the principal crops, but corn has failed to produce profitable yields in years of low rainfall.

Carleton Prairie

Three miles southeast of Carleton there is a nearly level upland prairie of about 40 acres. A broad, shallow ravine extends diagonally across it. The soil is Crete silt loam. The topsoil is dark brown to black and coarsely granular. Lime accumulations are generally present at depths of 2-3 ft. A poorly developed claypan occurs throughout.

Vegetation was of the mixed-bluestem type. Little bluestem furnished 50-85%, big bluestem 50% on low ground but often 20% elsewhere. The percentages at the western stations were obtained by repeated estimations and by data from numerous square-meter quadrats. Little bluestem showed a tendency to form small, distinct bunches rather than the usual sod-mat type and its stand was rather open. Even where big bluestem was best developed the sod was open, and Indian grass, switchgrass and Canada wild-rye occurred in small amounts; little bluestem was also usually intermixed. There were a few small areas of blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). Western wheatgrass was nearly confined to the swale where locally it formed a fourth to a third of the cover. Here a definite claypan was present at depths of about 10 to 28 in. This limited its root penetration to 3.5-4 ft. Over the area roots of bluestem grasses reached depths of 4-5 ft.

Junegrass was a constant component of the vegetation, in amounts of 3-6%, as were also Scribner's panic grass, Wilcox' panic grass, and side-oats grama in small amounts. Kentucky bluegrass was absent over much of the area but occurred locally in amounts of 5-15%; tall dropseed (*Sporobolus asper*) and six-weeks fescue (*Fes-*

tuca octoflora) occurred sparingly, and needlegrass only rarely.

The cover of vegetation was not only more open than usual but also the midsummer height of foliage was 6-8 in. less than in the preceding prairies. Nearly all tall, coarse forbs were absent and societies were fewer and poorer developed. There were only about 35 species of perennial forbs.

Hebron Prairies

Several areas of prairie were studied near Hebron, Nebraska. They occurred on rolling upland topography. The soil is Nuckolls silt loam into which water infiltrates readily, and one of good water-holding capacity. It is a deep Chernozem; carbonate accumulations occur at about 4-4.5 ft.

The prairie consisted largely of little bluestem, usually of the bunch grass type intermingled with 5-20% of big bluestem on the uplands, but on the drier slopes with a high percentage of side-oats grama and blue grama. Buffalo grass was rare but Junegrass and many species of forbs were abundant. Kentucky bluegrass occurred in small amounts more or less throughout the understory. Switchgrass and Indian grass occurred sparingly, mostly with big bluestem where it was dominant in ravines. Needlegrass was present in only small amounts. Western wheatgrass (*Agropyron smithii*) and tall dropseed grew on a few eroded banks of knolls.

The vegetation was better developed, species of forbs were greater in number, and societies were more plentiful than at Carleton. The openness of the cover, the presence of the short grasses, and the abundance of side-oats grama all indicated an approach to the Mixed Prairie of the Great Plains.

Belleville Prairies

Four miles east of Belleville, Kansas, there is a 30-acre prairie that is typical of several others nearby, which were also examined. The topography is rolling to hilly, and native grassland covers long east, west, and north slopes. A well-developed broad ravine is also present.

The pervious black loam soil is derived from soft limestone materials. The lime rock occasionally lies within 3-4 ft of the surface. At about 12 in. the topsoil gives way first to light brown, and then to yellow, clayey subsoil, which is less permeable. It is a deep soil with good water-holding capacity; both soil and subsoil are neutral in reaction.

This prairie was first studied in 1931. The lowest part of the ravine bore a pure stand of prairie cordgrass and several species of tall, coarse forbs. Bordering the cordgrass were excellent stands of big bluestem with a little Indian grass, and with switchgrass and Canada wild-rye on the wetter margins. There was a good understory of Kentucky bluegrass. A small patch of western wheatgrass grew in only one place. The higher land on all slopes was dominated by little bluestem with about 15% Junegrass and a considerable amount of big bluestem. No needlegrass was found. The steep portions of the hills showed almost pure alternes of buffalo grass and blue grama. Throughout these, as well as throughout the bluestem sod, side-oats grama was well distributed.

Height of little bluestem varied from 12 in. where it occurred in bunches on upper slopes to 18 in. in the sod-mat type on lower ground. Even in the best stands on lowland, the tall grasses were usually 1 to 3 ft shorter than those in eastern Kansas and Nebraska. Forbs were of considerable abundance but societies were few and less well developed than eastward.

Prairies examined near Concordia and westward to Montrose were similar to the preceding.

Montrose Prairie

The Montrose prairie, three miles south of Montrose, Kansas, consisted of about 60 acres of moderately rolling land with some nearly level areas and shallow ravines. The soil, except in the ravines, is Hastings silty clay loam. The 6 in. layer of topsoil is a dark, pervious mantle of silt loam underlain by a subsoil consisting of about 20 in. of grayish to light brown, slightly compacted, silty clay loam above unweathered loess. Roots of grasses and forbs penetrated deeply.

Little bluestem composed 65 to 80% of the cover on upper slopes and hilltops; big bluestem and Indian grass were intermixed 5-20% in the little bluestem type. Little bluestem occurred in both the sod-mat and bunch form. On the lower protected slopes and bottoms of ravines big bluestem, intermixed with Indian grass, had nearly complete possession. Higher, level ground was shared more or less equally by tall grasses and little bluestem. Side-oats grama composed 10-15% of the cover in places, and with Junegrass was common, especially on dry slopes. Scattered spears of western wheatgrass, tufts of buffalo grass and blue grama were persent but nowhere abundant. Small amounts of Kentucky bluegrass and six-weeks fescue were found. Switchgrass occurred sparingly in the wetter draws. Some bunches of tall dropseed and more often those of sand dropseed (*Sporobolus cryptandrus*) were present. No needlegrass was seen, and prairie dropseed, as in the preceding western prairies, was absent.

A few of the 44 species of forbs formed well developed societies but few tall, coarse plants were present.

Prairies near Nelson

Several areas of prairie about 5 miles northeast of Nelson, Nebraska, were repeatedly examined before the great drought of 1933. Topography varied from level to rolling. The soil was mostly Crete silt loam. Vegetation was of the mixed bluestem type. The more arid climate was indicated by the great amount of little bluestem and by its poorer development, by increasing amounts of side-oats grama and short grasses, and by the occurrence of several species of grasses and forbs from the Great Plains.

On many of the level or slightly sloping uplands, little bluestem, either in the bunch or sod-mat form, composed 80% or more of the cover. In midsummer it was only 10-12 in. high. In other places there was a mixture of 5-15%, and sometimes more, of big bluestem. Elsewhere, as on lower slopes, the amount of big bluestem increased to 40% or more. But on low ground where one would expect to find good and nearly pure stands of this tall grass, half or nearly half of the cover was composed of mid grasses. Even locally where big bluestem occurred alone, the stands were not dense, and in midsummer the grass was only about 15-18 in. tall.

Stands of little bluestem in drier places were often interrupted by alternes of blue grama, buffalo grass, and bunches of tall dropseed. Some dry knolls were occupied in part by western wheatgrass, sand dropseed and Junegrass. Side-oats grama was scattered throughout and was often 5% or more in local abundance. In some places six-weeks fescue, tumblegrass (*Schedonnardus paniculatus*) and bromegrass (*Bromus tectorum*) were intermixed with the other grasses. Low-growing panic grasses and penn sedge occurred in their usual 1-5% abundance. Switchgrass and Canada wild-rye grew only in ravines and were never abundant. Indian grass rarely exceeded 1-3% in amount even on lowland. Bluegrass was found, usually under big bluestem, but it was nowhere abundant. Throughout the several prairies, totaling many acres, a rather low and continuous, but sometimes thick, cover of grass prevailed. Forbs were relatively few and societies only moderately well developed.

Prairies near Superior, Nebraska and across the state line southward in Kansas were so similar to those at Nelson and Montrose that separate description seems unnecessary. It should be pointed out, however, that some were even more xeric than any of the preceding.

Summary of Grasses

Little bluestem was the most abundant species. It usually composed 60 to 85% of the grasses. Its tendency to occur in bunches was pronounced and the bunches were often less filled with stems than similar ones eastward. Big bluestem dominated the lower land but its stands were less dense than eastward and sometimes contained much mid grass. Switchgrass, Indian grass, and Canada wild-rye were almost confined to lowland and did not occur in great abundance. Needlegrass and western wheatgrass were found rarely. Kentucky bluegrass was not abundant, sometimes absent, and grew mostly under big bluestem. Junegrass and Scribner's panic grass were far more abundant than eastward. Patches of blue grama and buffalo grass, often rather extensive, grew on the driest sites. Here tall dropseed, sand dropseed and six-weeks fescue were also found. Tumblegrass, purple three-awn and plains muhly (*Muhlenbergia cuspidata*) were sometimes present. Side-oats grama was widely spread and sometimes, intermixed with little bluestem, composed 10-15% of the cover. The total cover of grasses was less dense, foliage of mature mid grasses was 6-8 in. shorter and that of tall grasses 1-3 ft shorter than eastward. Yield was considerably reduced.

Prairie Forbs

Species of forbs were much less abundant in the Loess Plains area. Only 6 species formed abundant and widely spread societies of the first class (Fig. 4). These were as follows:

Amorpha canescens	Lead plant
Antennaria neglecta	Prairie cat's-foot
Aster ericoides	Many-flowered aster
Erigeron strigosus	Daisy fleabane
Schrankia nuttallii	Sensitive briar
Solidago mollis	Velvety goldenrod

Velvety goldenrod is a xeric western species which was not listed in the preceding prairies. The others occurred abundantly eastward and, except for sensitive briar, ranged widely.

Species in the following list were of intermediate rank.

Artemisia ludoviciana	Sage
Callirhoe alceoides	Poppy mallow
Kuhnia eupatorioides	False boneset
Liatris punctata	Blazing star

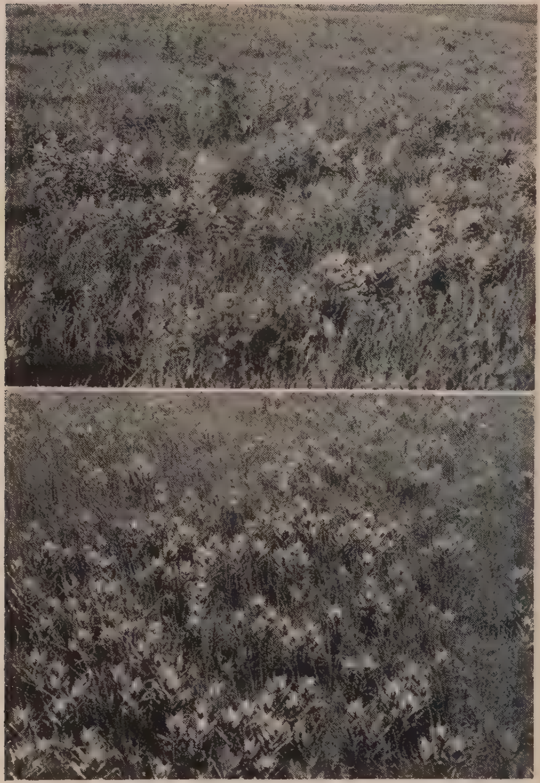

FIG. 4. Characteristic societies of forbs on the Loess Plains. (upper) *Amorpha canescens* and (lower) velvety goldenrod (*Solidago mollis*) in midsummer.

Linum sulcatum	Grooved flax
Psoralea argophylla	Silver-leaf psoralea
Senecio plattensis	Prairie ragwort
Solidago missouriensis	Missouri goldenrod

Three species occurred in the same rank and 4 were of lower rank, eastward. One, prairie ragwort, was not listed.

All the species that follow were of low rank. Those with an asterisk were not observed in the Drift-Loess Hills.

*Abronia fragrans**
Acerates angustifolia
Acerates viridiflora
Achillea millefolium
*Allium drummondi**
Allium mutabile
*Anemone caroliniana**
Apocynum cannabinum
*Asclepias pumila**
Asclepias sullivantii
Asclepias verticillata
Astragalus crassicarpus
*Callirhoe involucrata**
*Chrysopsis villosa**
Cirsium undulatum
*Comandra pallida**
*Dalea enneandra**
Lygodesmia juncea
*Microseris cuspidata**
Oenothera biennis
Oenothera serrulata
Onosmodium occidentale
*Opuntia macrorhiza**
Oxalis stricta
Oxalis violacea
*Oxybaphus linearis**
*Oxytropis lambertii**
Penstemon cobaea
*Penstemon grandiflorus**
Petalostemum candidum
Petalostemum purpureum
Physalis lanceolata
*Plantago purshii**
Polygala verticillata
Delphinium virescens
Euphorbia dentata
Galium aparine
*Gaura coccinea**
Gentiana puberula
Glycyrrhiza lepidota
*Haplopappus spinulosus**
*Hedeoma hispida**
Helianthus laetiflorus
Helianthus maximiliani
Hieracium longipilum
*Hymenopappus tenuifolius**
Lespedeza capitata
Liatris punctata
Liatris scariosa
Liatris squarrosa
Lithospermum canescens
Lithospermum incisum
Lomatium foeniculaceum
Lomatium orientale
*Lotus americanus**
Potentilla arguta
Psoralea argophylla
Psoralea tenuiflora
Ratibida columnifera
Rhus radicans
Rosa suffulta
Rudbeckia hirta
Salvia pitcheri
Silene antirrhina
Sisyrinchium angustifolium
Solidago altissima
Solidago rigida
Solidago speciosa
Specularia perfoliata
*Spermolepis inermis**
*Sphaeralcea coccinea**
Thelesperma gracile
Tradescantia bracteata
Vernonia baldwini
Vicia americana
Viola pedatifida

This list of 76 species is fairly long; added to the species of higher rank it totals 90, as compared with a total of 131 eastward. This results in part from the presence of 21 species common to Mixed Prairie which were not found eastward. The number of species alone, however, does not give an accurate picture of the much less abundant forb population. Tall-growing species were few, societies were not abundant, and they were much less well developed in this drier western area.

Discussion

Differences between the vegetation west of the Flint Hills and east of them was recognized by an early botanist (Schaffner 1926). He had been intimately acquainted with the prairies of Kansas since 1871. He states that "in passing from Clay County [see Fig. 1] to Douglas County [adjoining Jefferson County on the south] a distance of 100 miles, one experienced a remarkable change in the character of the species on all the ordinary and higher levels, while the transition from Douglas County, Kansas, to Franklin County, Ohio, a distance of about 600 miles, is much less marked."

The greater aridity of the western prairie was shown in many ways. In prairies of the Drift-Loess Hills that had been heavily pastured for several years, the bluestems were replaced by Kentucky bluegrass and with varying amounts of shrubs, such as smooth sumac, coralberry, and roughleaf dogwood. But on the Loess Plains the bluestems usually gave way under grazing to short grasses, blue grama and buffalo grass. Even the shallow ravines became clothed with buffalo grass, although bluegrass sometimes grew in the more moist, deeper ones.

As a result of the severe and prolonged drought of 1933-40 Mixed Prairie grasses and forbs moved eastward 100-150 mi. and actually replaced the bluestems and most accompanying species in mowed True Prairie of the Loess Plains. But eastward from the 32 in. isohyet, while the prairie suffered some damage, it was relatively slight in comparison and recovery was complete (Weaver 1943).

The change from True Prairie to Mixed Prairie westward does not result in the complete replacement of the bluestems. They still occur in sandy soil or other favorable sites, but their dominance is usually replaced by that of western mid and short grasses. Those shown in Figure 5 are representative. All are deeply rooted and are highly drought evading or drought resistant. The short grasses are short only above ground. Their root to top ratio is much greater than that of the mid grasses. A similar trend occurs between roots and tops of dry-land forbs. The appearance of these grasses in the western edge of True Prairie and their increase in abundance is clearly indicative of a less mesic environment than in the excellent bluestem prairies of the Drift-Loess Hills.

SUMMARY

The Drift-Loess Hills of northeastern Kansas and southeastern Nebraska are not unlike the Loess Plains in topography, except that the hills are more pronounced in the east and more level land alternates with lower hills in the Loess Plains westward. Both have highly productive soils. Eastward glacial boulders and limestone outcrops are common. On the Loess Plains the bedrock is nearly completely covered with loess. Soils in the Chernozem Zone westward are somewhat less productive than those in the Brunizem Zone eastward, not because of lack of innate fertility, but because of reduced precipitation. Precipitation ranges from 29-34 in. in the east to 27-28 in. in the west. Since altitude and latitude are similar, the length of the growing season is nearly the same. Humidity is lower and drying winds are higher and more frequent in the west. Evaporation is also greatly increased westward and periods of drought are more frequent and of longer duration.

Both areas of True Prairie are composed of the *Andropogon scoparius* type on uplands and the *A. gerardi* type on lower slopes and low, level lands. On mid slopes the two bluestems may intermix about equally. In the west, the little bluestem type occupies a greater portion of the prairie than eastward, the grass more often occurs as bunches and frequently intermixes with big bluestem on lower slopes. *Sporobolus heterolepis* is common and sometimes locally abundant eastward; it did not occur at the western stations. *Stipa spartea* was common but rarely abundant eastward; it was usually absent in the west. *Panicum virgatum* and *Sorghastrum nutans* were of considerable abundance (5-20%) eastward and ranged widely; westward they were much less abundant and more restricted to ravines and low ground.

Midsummer foliage level of little bluestem was often 16-24 in. in the east but 8-18 in. westward; similar average heights of big bluestem were 18-26 and 26-36 in. The general foliage cover was not only higher but also considerably denser eastward. Westward, *Bouteloua curtipendula* and *Koeleria cristata* became far more abundant, and the low-growing *Panicum scribnerianum, P. wilcoxianum* and *Carex pennsylvanica* greatly increased in amount. Great Plains grasses, not observed in mowed prairies eastward but common westward, were *Bouteloua gracilis* and *Buchloe dactyloides*. The following species of Mixed Prairie grasses also occurred in some western mowed prairies: *Agropyron smithii, Aristida purpurea, Festuca octoflora, Schedonnardus paniculatus* and *Muhlenbergia cuspidata*.

In the bluestem prairies of northeastern Kansas and southeastern Nebraska 65 to 100 species of

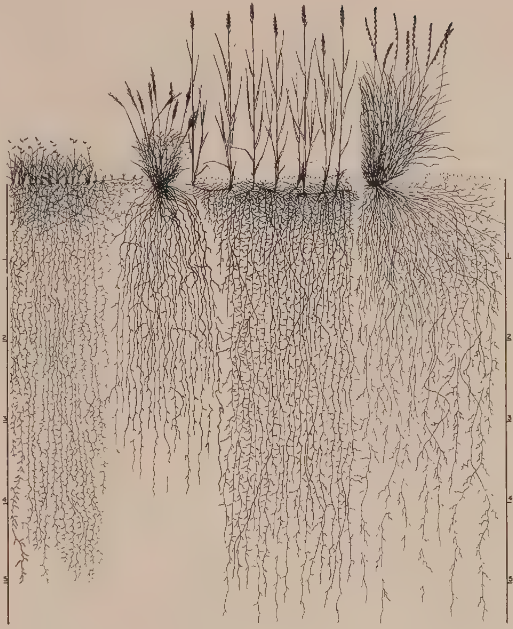

FIG. 5. Tops and roots of dominant grasses common to mixed prairie. Only those parts in a strip 1 in. wide are shown. From left to right are buffalo grass (*Buchloe dactyloides*), (height and depth of which is very similar to that of blue grama), purple three-awn (*Aristida purpurea*), western wheatgrass (*Agropyron smithii*) and side-oats grama (*Bouteloua curtipendula*).

forbs were usually observed in selected prairies 40-60 acres in extent. Westward the lists were shorter, 35 to 60 species. Forbs were greatly reduced in stature westward, there were fewer and less well developed societies, and numerous species common to Mixed Prairie were present.

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ASPECTS OF THE ECOLOGY OF THE PACIFIC SLENDER SALAMANDER, *BATRACHOSEPS PACIFICUS*, IN SOUTHERN CALIFORNIA

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In California south of Santa Barbara County only four terrestrial salamanders are found, two of which are slender salamanders of the genus *Batrachoseps*. The present work is limited to a study of the ecology of the Pacific slender salamander, *Batrachoseps pacificus* (Cope).

Interpretations of the taxonomic entities within the genus *Batrachoseps* have varied widely. Hendrickson (1954) came to the conclusion that *B. pacificus* was not a valid species and reduced it to subspecific rank in the species *attenuatus*. The writer does not subscribe to his arguments and prefers to follow Campbell (1931), Lowe and Zweifel (1951), Stebbins (1951), and Stebbins and Lowe (1949) in regarding the large, light-colored forms of the islands and coastal plain of southern California as *B. pacificus*. This conclusion was reached as a result of the collection of over 3,000 salamanders of the genus from the southern California mainland.

B. attenuatus typically inhabits the foothills and mountain canyons, usually associated with live oaks and/or chaparral, while *B. pacificus* inhabits the more level regions within the drainage systems of the Los Angeles, San Gabriel, and Santa Ana Rivers.

Relatively little has been written concerning the ecology of the genus *Batrachoseps*. The most comprehensive ecological report is that of Hendrickson (1954) on *B. attenuatus* in northern California. The present work is concerned with an intensive study of a marked population of *B. pacificus* in Santa Monica, Los Angeles County, California. The study extended from November 1955 through July 1956.

Area of Study

The population study area is in a typical residential section of Santa Monica. This city is located on the Los Angeles coastal plain at an elevation of approximately 200 feet above sea level. Upper Sonoran life zone conditions prevail and native vegetation in this region at one time consisted of coastal sage scrub and chaparral (Munz and Keck 1949). Today, the entire metropolitan Los Angeles region is heavily pop-

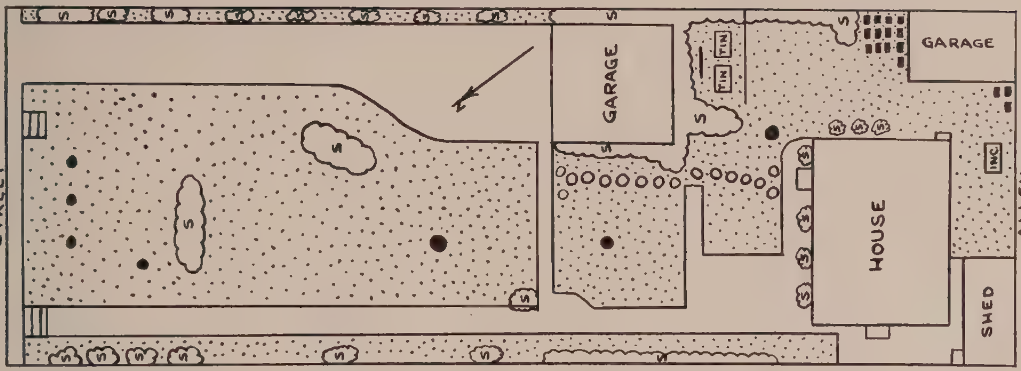

FIG. 1. Map of area of study of marked *Batrachoseps pacificus* at Santa Monica, Los Angeles County, California, December, 1955. Stippled area, lawn; unstippled area, cement; S. shrubbery; solid circles, trees; INC., incinerator. Scale: Large garage is 18 ft. square.

ulated and little natural vegetation remains. For many miles surrounding the study area there are now residential and industrial districts, and no native plant communities exist.

The site chosen for study was a typical residential lot measuring approximately 7700 square feet (Figure 1). Of that sample plot, 600 square feet were occupied by a house and 700 square feet by other buildings. The vegetation was comprised largely of lawn bordered by various shrubs and herbaceous annuals, sometimes forming very thick growths. A few trees provided patches of shade. A paved road and alley bordered the study plot on the east and west.

Miscellaneous pieces of bricks, boards, and other surface objects were scattered over some sections of the yard and these provided shelter for many salamanders. Each surface object was given an identification number. There were approximately 140 of these marked surface shelters as well as numerous smaller, unmarked items of debris which rarely harbored salamanders. The premises were not cared for as carefully as most gardens in the neighborhood. The lawn was mowed only twice during the period of study. Occasionally, drastic changes were made in the vegetation and physical surroundings of the yard. It was thus possible to gain an insight into salamander activity under both disturbed and relatively undisturbed conditions.

Reptilian associates of *B. pacificus* were the Western fence lizard (*Sceloporus occidentalis*) and the San Diego alligator lizard (*Gerrhonotus multicarinatus webbi*). Also present was a small population of *B. attenuatus*. Approximately 20 of the latter were captured during the study. Residential gardens along the coastal plain are apparently unsuitable habitat for this species.

Climate

The climate of coastal southern California is of the Mediterranean type. Summers are long and warm without precipitation. Summer thunderstorms are rare except in the higher mountains and certain foothill regions. Major precipitation occurs during the winter with rains commencing in October or November and occuring intermittently through the spring. The heaviest rainfall normally occurs in January. Along the coastal plain in the Los Angeles region precipitation in the form of rain approximates 15 inches annually. In foothill regions and in the Santa Monica Mountains precipitation approximates 25 inches annually. Snow may fall at these and higher elevations. Thus, climatic conditions favorable for salamander surface activity normally extend from October through June or July. At other times *Batrachoseps* is rarely found on the surface.

Fog is of common occurrence and the resulting higher relative humidity may extend the time of favorable conditions by reducing the evaporative rate. Fog also decreases the amount of incident light and, when it is sufficiently dense, salamanders have been found on the surface during mid-afternoon. During the winter, fog and overcast conditions will frequently persist for weeks at a time. Within this coastal plain habitat freezing temperatures occur infrequently.

METHODS OF STUDY

Marking

In order to study movement and growth of individual salamanders, toes were excised in various combinations. Each leg was designated by a letter and each toe by a number. Because of the small size of the fourth toe only the 3 largest toes were numbered. However, to avoid possible confusion, both the small toe and the adjacent one were excised. Thus, a typical salamander might be designated by the toe combination of A3B2C3D1. Amputations were performed with a sharp razor blade.

An attempt was made to mark the salamanders at the spot where they were discovered but, owing to their small size, the poor light conditions prevailing, and the resultant chance for errors, this method was soon discarded except in the case of the largest individuals. Smaller ones were taken into a lighted room for positive marking or identification. The entire process of removing the salamander from its original site to the lighted room a few feet away, marking and identifying, and returning to the place where it had been found, on the average, took 2 minutes or less.

In only one case was complete regeneration of a toe noted.

Measurement

The study was of such short duration that relatively little growth was noted. One individual grew 5 mm in body length during the span of the study but most salamanders remained the same length or gained only 1-2 mm. Tail growth and regeneration visually exceeded the increase in body length. This was particularly true if the regenerating tail had been severed near its base. Approximately a third of those salamanders from which valid measurements were secured lost their tails at some time during the study. Autotomy is such a common occurrence as to suggest that it may be an important defensive mechanism for *Batrachoseps*.

Census Procedure

Studies were conducted mainly at night from 6:00 to 11:00 p.m. although approximately 4 daytime observations were made each week in order to ascertain whether *Batrachoseps* were ever active diurnally. During the first 2 months of the study a search was made nearly every night, and, during the latter part of the study, visits averaged three evenings a week between approximately 7:00 and 9:00 p.m. On several occasions spot checks were made shortly before sunrise to note activity at that time. As nearly as possible the area was searched completely on each visit. The study plot was checked 98 times at night and on numerous occasions during the day.

Whenever a salamander was discovered, its location was noted in relation to the nearest numbered object or prominent landmark. After examination, a surface object was always carefully returned to its original location. In order not to damage the habitat search was never made in the leaf litter beneath shrubs.

Numbers

A total of 539 salamanders was marked and of these 375 were recaptured at least once (Table I). The average number of salamanders found on each visit was 22, with a range of 0-62 (Figure 2).

TABLE I. Recapture frequencies of marked *Batrachoseps*, December, 1955 to May, 1956

Number of times captured	Number of salamanders
1	164
2	84
3	65
4	56
5	37
6	24
7	17
8	22
9	20
10	6
11	10
12	12
13	8
14	3
15	2
16	3
17	2
18	2
19	0
20	1
21	1

ENVIRONMENTAL FACTORS

Light

Light appears to have a great influence upon the activities of *Batrachoseps*. Although many searches were made, salamanders were never discovered active in full sunlight. As daylength increased toward summer the salamanders became active at progressively later hours. When the sky was overcast, however, *Batrachoseps* would become active before complete darkness. At times cloud- or fog-subdued light permitted early afternoon activity. Neither bright moonlight nor the quite bright reflection of city lights on low ceiling clouds or fog affected surface activity. In general, slender salamanders can be said to be photophobic to strong illumination.

Temperature

Knowledge of the temperature relationships of an ectothermic animal is of paramount importance for an understanding of its ecology. While numerous studies have been devoted in recent years to the thermal ecology of fishes and reptiles, sufficient consideration has not yet been given to this aspect in most amphibian ecological studies,

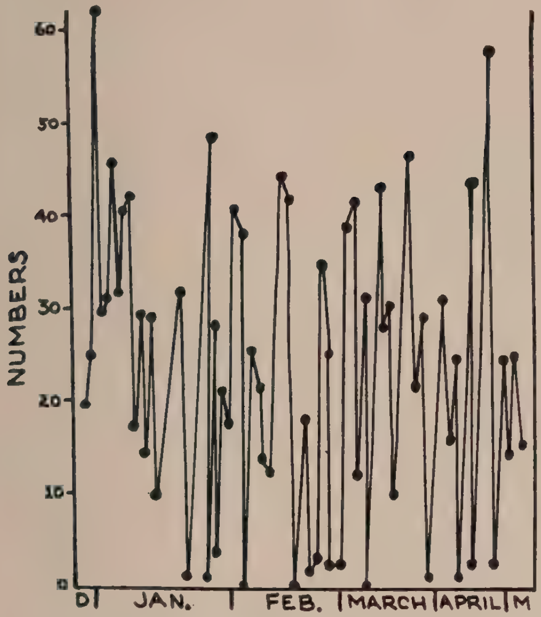

FIG. 2. Number of salamanders active in the population study area, December, 1955 to May, 1956.

if one excludes studies of temperature effects on embryonic anurans. Stebbins (1954) has published data on activity temperatures for *Ensatina eschscholtzi* and Henrickson (1954) recorded similar data for *Batrachoseps attenuatus*. Environmental temperatures for a variety of plethodontid salamanders were studied by Bogert (1952). Studies on the upper thermal limits of salamanders have been conducted by McFarland (1955), Stebbins (1954), and Zweifel (1957).

All temperatures were taken with a quick registering Schultheis thermometer. Air temperatures were taken at a height of 3 to 5 mm (depending upon the size of the salamander) above the substrate upon which the salamander was first noted. Care was always taken to obtain temperatures not unduly influenced by radiation and conduction to or from the human body.

Substrate surface temperatures were secured by inserting the thermometer horizontally beneath the surface material just enough to barely cover the bulb. Even with this technique substrate temperatures are not actually those of the soil surface but they do approximate them closely (Geiger 1950). Body temperatures could not be secured in the field because of the small size of the salamanders and the slippery skin which made it difficult to hold the animals without injuring them. Furthermore, many of the temperature data were secured from the population study area where it was advisable not to handle excessively or otherwise disturb the salamanders.

In a laboratory experiment in which salamanders were placed upon soil of various temperatures between 1° and 20° C and left until thermal equilibrium with their environment was attained, it was shown that the body temperature very closely approximates that of the soil with which the salamanders are in contact. *Batrachoseps* are usually found with most of their ventral surface in contact with the ground or only a fraction of a millimeter above the substratum. Their very small limbs preclude their rising more than a few millimeters above the substratum.

The nocturnal habits of *Batrachoseps* and their use of subterranean diurnal retreats precludes their being subjected to extreme thermal conditions. Stebbins (1954) has shown that environmental temperatures in the habitat of *Ensatina* never approach the critical thermal maximum for that species. The critical thermal maximum has been defined by Cowles and Bogert (1944) as the point at which locomotor activity becomes disorganized and the animal is incapable of escaping from conditions that, if continued, will lead to death. In relation to the thermal tolerances of *Ensatina*, Stebbins (1954) found the curve based on the body temperatures of active salamanders to lie closer to the critical minimum than to the critical maximum temperature.

The data presented here represent the environmental temperature range under which *Batrachoseps* are usually active and the extreme temperatures tolerated may well be extended by further work. Temperature data secured during the present study tend to support the findings of Bogert (1952). Populations of slender salamanders of both species occurring in widely divergent areas were found in apparently comparable stages of activity under variable temperature conditions. *Batrachoseps* seemed equally active and coordinated at any thermal level within the range tolerated.

During the summer, when high environmental temperatures prevail, slender salamanders are not active on the surface. Because high temperatures and desiccation of the ground occur simultaneously this inactivity cannot be attributed solely to temperature. It should be emphasized that temperature fluctuations in the damp and shaded environment usually frequented by *Batrachoseps* are slight.

Figure 3 gives the substrate temperatures secured from the site of capture of over 400 *B. pacificus*. Recorded substrate temperatures for

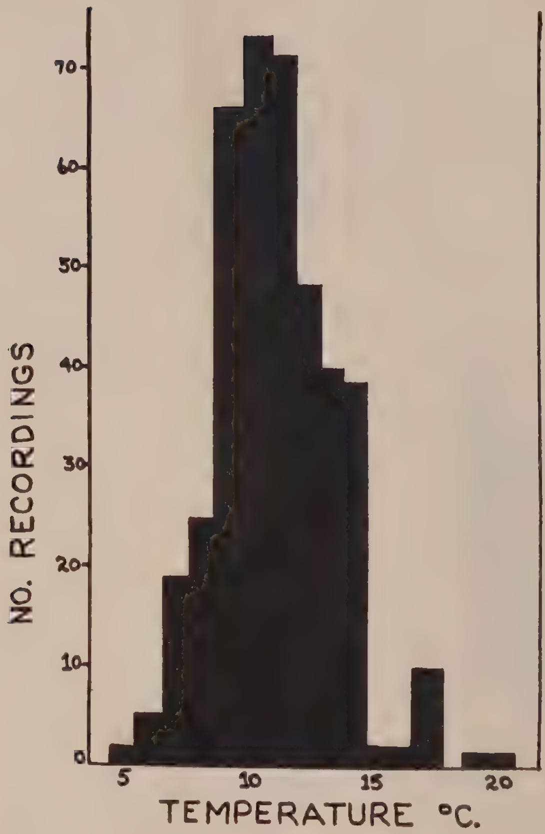

Fig. 3. Substrate temperatures recorded at the site of capture of individual *Batrachoseps pacificus* in the population study area, November, 1955, to May, 1956.

B. pacificus were secured during the nocturnal observations of these salamanders in the study area. These data are useful only for illustrating the range of environmental temperatures most frequently encountered by slender salamanders in their surface wanderings. As with the terrestrial plethodontid species studied by Bogert (1952), *Batrachoseps* was not discovered on soil with a higher temperature than 21° C. At the opposite extreme, no salamanders were discovered on soil with temperatures lower than 4° C. Although the surface of the soil occasionally freezes in the habitat of *Batrachoseps*, they can escape to lower, warmer depths. The soil rarely freezes in the area where these studies were conducted, and the lowest substrate temperature taken where a salamander was active was 5.9° C.

Because *Batrachoseps* are active nocturnally, direct insolation can be ruled out as a source of body heat. Quiet air at the level of the salamander's body closely approximates the soil temperature (Figure 4). In only one instance did the difference between substrate and air temperature exceed 2° C and in the majority of instances the difference was only a fraction of a degree. Being in intimate contact with the substratum, *Batrachoseps* probably derives most of its body heat from the ground.

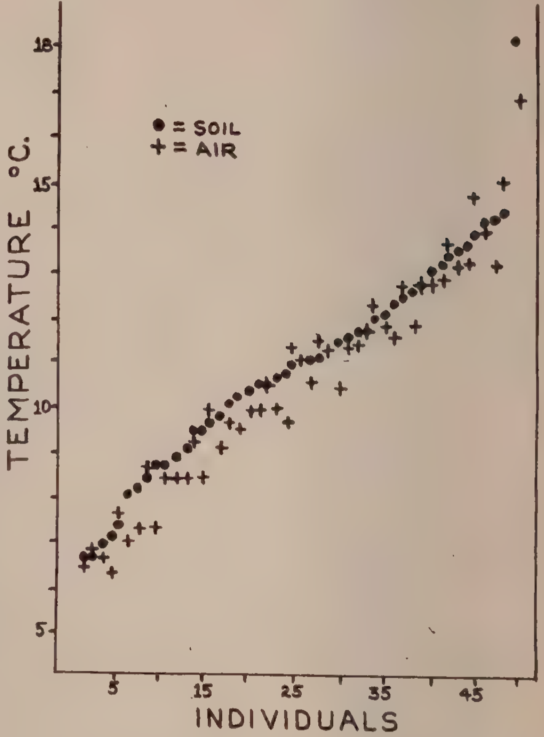

Fig. 4. Thermal environment of *Batrachoseps pacificus* at the population study area, November, 1955, to May, 1956.

Moisture

Of all the physical factors observed in the environment of *Batrachoseps*, the one having the most limiting effect on activity appeared to be moisture. Wholly terrestrial species are particularly susceptible to desiccation and must, by locomotor adjustments, maintain access to moist conditions. To assist in respiration the skin must not be damaged by drying. Because of its thinness and vascularity the skin readily takes up water from the moist surfaces with which it comes in contact.

The effect of size upon the rate of water loss has been adequately demonstrated with amphibians (Stebbins 1954, Thorson 1955). Small animals lose water more rapidly than larger ones because of the relatively greater body surface in the former. Thorson showed that tolerance to water loss was greater in small amphibians than in larger ones. This greater tolerance to water loss in small amphibians seems directly related to the relatively greater amount of body water initially present. The disadvantage of a rapid evaporative loss offsets the advantage of a high tolerance to water loss, however.

In order to determine the total body water, several *B. pacificus* were kept for 24 hours in a closed plastic chamber lined with saturated paper toweling and with an inch of water in the bottom. It was assumed that during that period the salamanders would have absorbed all possible body water although, as has been shown by Adolph (1932) and Thorson (1955), amphibians are constantly losing water by evaporation even in a saturated environment. After the 24 hour period the salamanders were removed, weighed, and placed in an oven at 110° C for 8 hours. A comparison of weight before and after desiccation is shown in Table II. The average of the original body weight lost was 80.6% with a variation ranging from 79.7 to 81.5%. The smaller salamanders contained relatively more body water than larger ones.

TABLE II. Total body water content of *Batrachoseps pacificus*

Weight before desiccation (gm)	Weight after desiccation (gm)	Percentage of original body weight lost
3.20	0.65	79.7
3.20	0.65	79.7
2.70	0.50	81.5
1.60	0.30	81.2
1.00	0.20	80.0
0.80	0.15	81.3

An attempt was made to determine the sublethal dehydration point (vital limit) of *B. pacificus.* The animals were hydrated for 24 hours as previously described. In this case also it was assumed that the salamanders had absorbed the maximum complement of body water prior to desiccation. After being taken from the hydrating chamber and weighed the salamanders were placed upon a piece of filter paper in a calcium chloride desiccator in air at a temperature of 21-22° C. They were observed at 20 to 25 minute intervals and removed, weighed, and replaced in the hydrating chamber when their appearance and behavior indicated that they had approached a critical level of desiccation. With the exception of one salamander which dried very quickly (14 minutes), they required from 30 minutes (the smallest individual) to 320 minutes (the next to largest) to reach their critical level of water loss (Table III). *B. pacificus* were able to withstand an average loss of body water amounting to 34.7% of original body weight without apparent harmful effects.

TABLE III. Vital limit of water loss in *Batrachoseps pacificus*

Weight before desiccation (gm)	Weight after desiccation (gm)	Percentage of original body weight lost	Time of desiccation (min)
0.50	0.35	30.00	155
1.65	1.15	30.30	65
1.70	1.15	32.35	235
0.30	0.20	33.33	30
1.45	0.95	34.48	260
0.85	0.55	35.29	115
2.80	1.80	35.71	95
0.65	0.40	38.46	195
2.45	1.50	38.78	320
0.90	0.55	38.89	205

Salamanders weighing less than a gram (original weight) showed a greater tolerance to water loss than did larger individuals. The smaller specimens, however, took an average of 140 minutes to reach their vital limit while the larger salamanders averaged 195 minutes.

Hall (1922) found that *Ambystoma maculatum* survived a body water loss of 41%. Littleford, Keller, and Phillips (1947) found that *Eurycea b. bislineata* and *Desmognathus f. fuscus* both survived average losses of about 18%. *Plethodon c. cinereous,* the most terrestrial of the species studied, survived about 26% loss. Stebbins (1945) dug an adult *Ensatina eschscholtzi* from its aestivation site and found that, when placed on moist paper toweling, it absorbed water equivalent to nearly 40% of its total original weight.

To ascertain the ecological significance of this non-fatal dehydration capacity of *B. pacificus* an experiment was conducted to determine the amount of body water lost by *Batrachoseps* during their normal activities. From January 7 to 10, nineteen salamanders were captured and immediately weighed and hydrated as previously described. From the gain in weight after hydration it was possible to determine the approximate loss tolerated under field conditions (Table IV). The average water loss tolerated was 5.8% of the maximum body weight with a variation ranging from 0 to 21.2%.

From these data it seems probable that while *B. pacificus* may occasionally tolerate considerable loss of body water during its normal nocturnal wanderings, there remains a wide margin of safety.

During the early part of the study occasional determinations of relative humidity were made by an aspirating psychrometer placed 10-12 mm

TABLE IV. Water loss tolerated by *Batrachoseps pacificus* under normal conditions

Weight when captured (gm)	Weight after hydration (gm)	Water loss tolerated (%)
0.45	0.45	0.00
0.85	0.85	0.00
1.30	1.30	0.00
1.35	1.35	0.00
3.00	3.00	0.00
3.20	3.20	0.00
3.20	3.20	0.00
1.30	1.35	3.70
2.35	2.45	4.08
1.85	1.95	5.13
0.70	0.75	6.67
0.70	0.75	6.67
1.30	1.40	7.14
1.85	2.00	7.50
1.05	1.15	8.69
1.30	1.45	10.34
1.30	1.45	10.34
2.35	2.75	14.54
1.30	1.65	21.21

above the substratum. These readings alone appeared to be of little value in explaining differences in numbers of active salamanders. On evenings with turbulent air conditions, especially following a windy day with intense insolation, the surface of the soil would frequently become desiccated and salmanders would rarely be active. Under windy conditions with relative humidity as low as 27% or as high as 68% no surface crawling salamanders were discovered. Their susceptibility may be explained by the large surface area in proportion to mass. Turbulent air, particularly following a day of intense insolation, is a most important physical agent since it dissipates moisture from both the ground and from the skin of the salamanders, thus limiting nocturnal surface activity.

On a windy evening with relative humidity of 27% two small *Batrachoseps* were discovered dead and desiccated on the surface of the ground. It is assumed that they ventured too far from their retreats and were dried beyond their vital limit.

On evenings without wind numerous salamanders were usually active despite occasional relatively dry conditions. Under such conditions they have been found wandering about on sidewalks, streets, and dry soil when the relative humidity was as low as 54%.

Although fall rains initiate activity in terrestrial salamanders in southern California and trigger mass movement, *Batrachoseps* are active throughout the year in well watered city yards and other favorable locations, a fact that suggests lack of a strong innate cycle. During and immediately following the first autumn rains *Batrachoseps* becomes active in very large numbers. At that time they can be found wandering about on exposed surfaces such as cement sidewalks and paved roads.

The discovery of what is apparently the first known aestivation site of *B. pacificus* was reported to the writer by Mr. John Todd. During the summer (probably in July) of 1955, while excavations were underway for additional buildings on the Santa Monica High School campus, a "ball" of 6 very slimy salamanders was discovered in a cavity in moist soil at a depth of approximately 3 feet. Summer precipitation is rare and seldom wets the soil, therefore *Batrachoseps* normally must go into aestivation in late June or July and remain through the summer until the first heavy autumn precipitation allows surface activity. The writer is familiar with an instance in which a lawn was watered heavily in early September, a full month before the first fall rains, causing large numbers of *B. pacificus* to emerge.

These observations indicate that within extreme limits moisture is a more important limiting factor than temperature or light.

MOVEMENT OF INDIVIDUALS

Some type of territorial behavior has been found in each major class of vertebrates and in certain invertebrates. There have been few studies on movements of terrestrial salamanders (Gordon 1952, Hendrickson 1954, Stebbins 1954), although there are numerous reports on salientians. The advantages of a home range have been extensively discussed by Dice (1952) and throughout this discussion Dice's definition of a home range as "the area over which an individual animal habitually travels while engaged in his usual daily activities" has been followed.

Table I shows the recapture frequencies of marked *B. pacificus*. There were no returns for a third of the 539 marked salamanders and the remainder were sometimes recaptured as often as 21 times.

Since sex determination was not feasible no comparative data are available for movements of the sexes. Whenever it was convenient each individual was measured so that a comparison of movements by different size groups is possible. As might be expected, the larger the salamander the greater the distance traversed in its normal activities. Many of the small *Batrachoseps* would be repeatedly found under the same shelter. Hendrickson (1954) found a similar situation existing with *B. attenuatus*, and Stebbins (1954) recorded much the same behavior for small *Ensatina eschscholtzi.*

For *B. attenuatus,* Hendrickson (1954) records a home range of very limited surface area. Of 133 animals recaptured at least once, he found that 59% never changed shelter. In comparison, of the 375 *B. pacificus* recaptured at least once, 92% were recorded as having moved to other cover. Some of the travel was simply to nearby shelter but numerous salamanders made several moves of over 3 feet. Of those that moved over 3 feet the majority did so more than once. Thus *B. pacificus,* perhaps because of its larger size, has a much larger home range than does *B. attenuatus.*

As a generalization, Hendrickson (1954) concluded that unless other surface objects were located less than the normal cruising radius of 5 feet from the home object, *B. attenuatus* tended to return to spend the daylight hours beneath the home board. When surface objects were located farther than 5 feet from the home object the salamander would, upon reaching that object, remain there for varying lengths of time. Similar behavior was noted in certain instances with *B. pacificus.* Figure 5 illustrates several examples of individuals that seemed to have wandered beyond their usual home range, found a suitable microenvironment, and established a new home range. In most instances the salamander never returned to its original area.

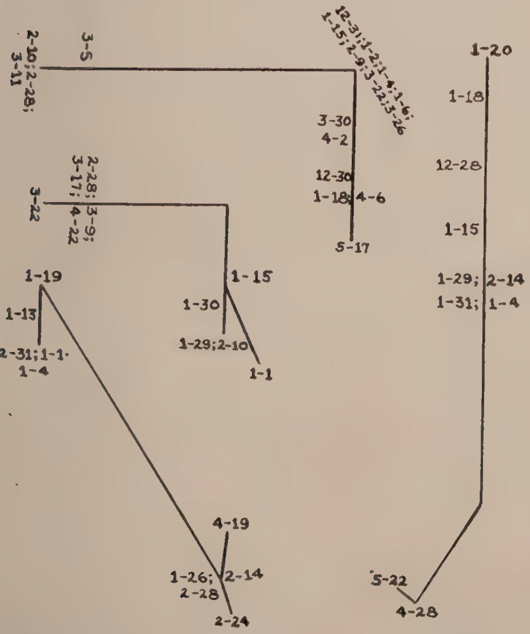

FIG. 5. Collection records of individuals of *Batrachoseps pacificus* which appeared to have two home ranges, December, 1955 to May, 1956. Numerals show dates. Scale: Total height of diagram represents 60 ft.

Some of these changes in home range can be attributed to seasonal variations in the vegetation. During times of the year when certain plant species are abundant, salamanders whose home range included that plant seem largely to restrict their activities to the proximity of the plant's shelter. Later, when the plants die or are pruned, some salamanders move and establish another home range. Normal gardening activities, such as weeding, planting, cultivation, and irrigation have a profound influence upon home range relationships. Most cases of changed home ranges in the study plot seem directly attributable to these man-induced habitat alterations. Since most of the regions where *B. pacificus* is now found are in areas where habitat changes by man are of a similar nature, this type of home range behavior is apparently of common occurrence.

No general statement can be made concerning the home range behavior of the Pacific slender salamander, as several patterns of behavior are apparent. The size and shape of the home range was usually directly dependent upon the microenvironment. Salamanders living in areas of abundant shelter, moist conditions, and favorable food species, tended to have smaller home ranges than salamanders in other areas. A review of some major factors influencing home range size has been presented by Stickel (1950).

Scattered throughout the area under observation were burrows of unknown origin but presumed to be old earthworm burrows enlarged by salamander use and water action. They were approximately 5 to 15 mm in diameter and descended vertically several centimeters. Early in the evening as many as 5 salamanders have been observed with their heads protruding from the same burrow. *Batrachoseps* commonly would remain in this position as long as 2 hours. If conditions favorable for surface activity did not materialize they would not completely emerge that evening. Very large concentrations of *Batrachoseps* are present in the vicinity of such burrow systems and these salamanders commonly have home ranges of relatively limited extent. Size of home range tends to be smaller in densely populated areas than in sparsely populated regions. Where burrows are scarce the population density is low and the salamanders wander in an irregular pattern, often changing their home base.

If approached near its home burrow, *Batrachoseps* rapidly retreats down its hole, usually entering head first. Such a salamander may lie exposed for some time with only the tip of its tail in the burrow and when retreating this acts as an anchor by which it can quickly pull itself backward to safety. During the daytime it is only rarely that these animals can be found under a surface shelter. It is believed that the majority spend daylight hours in subterranean chambers.

Batrachoseps occasionally makes extended excursions of short duration outside of the normal home range (Figure 6) but rapidly returns to the original site. Similar behavior has been reported for mammals (*Peromyscus*) and reptiles (*Terrapene c. carolina*) by Blair (1940) and Stickel (1950), respectively. Burt (1943) has said "Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range."

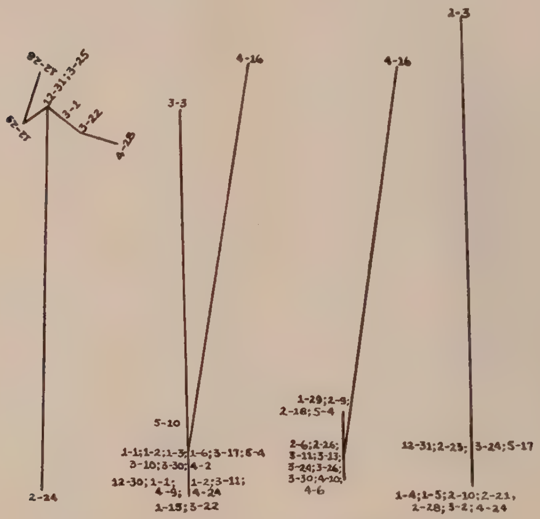

FIG. 6. Collection records of individuals of *Batrachoseps pacificus* which made extensive trips outside their home range, December 1955, to May, 1956. Numerals show dates. Extreme height of diagram represents 60 ft.

Stickel (1950) suggested that for box turtles these trips outside the home range were not random in direction. There was some evidence that this was also true for *B. pacificus.* Thus, the difference between the possession of 2 home ranges (Fig. 5) and travels away from the home range in a non-random direction (Fig 6) is only one of degree, depending on the length of time spent in each area. These trips away from the home range are as yet unexplained.

Patterns of movement of certain individuals, chiefly juveniles, suggested the possibility that they were transients moving through the study area. These individuals exhibited apparently random movements and were seldom collected from the vicinity of an area more than a few times. Many salamanders were collected only once and, since most of these were from the peripheral areas of the study plot, it is believed that they represent individuals with home ranges barely entering the area.

When plotting home ranges it has been necessary to connect the several points of capture by a straight line. Using a trailing device in her studies on box turtles, Stickel (1950) found little relationship between the actual distance a turtle may travel in a day and the distance as indicated by a straight line measured between points of capture. Presumably, this generalization would also apply to *Batrachoseps.*

Nearly all observations were made relatively early in the evening and therefore it is possible that the salamanders were consistently collected near their diurnal shelter, thus leading to an underestimate of the actual home ranges. However, in all but one case, those salamanders collected on several visits shortly before sunrise were also within the bounds of the home range. Thus, it appears that *Batrachoseps* may traverse its home range within the period of a few hours and almost certainly within an evening, assuming favorable environmental conditions.

For 141 individuals that were captured at least 5 times, the average maximum distance of capture was 19.8 feet (Table V). These data included neither transients nor those having 2 home ranges nor having made trips outside of the home range. Thus, *B. pacificus* has a considerable larger home range than *B. attenuatus* (Hendrickson 1954).

TABLE V. Home range relationships of *Batrachoseps pacificus*

Maximum distance of capture (ft)	Number of salamanders
0-5	7
6-10	28
11-15	24
16-20	14
21-25	12
26-30	20
31-35	4
36-40	7
41-45	5
46 50	0
51-55	2
56-60	2

Territoriality has not been clearly demonstrated to exist in amphibians. The presence of numerous individuals of all sizes, and presumbaly of different sexes, in the small confines of a single burrow would tend to illustrate the absence of a territory in this species. The slender salamander shows social tolerance and even if from different areas they display no aggression when placed together. Likewise, when *B. attenutatus* are placed together with *B. pacificus* no aggressive behavior is exhibited. Home ranges may overlap in the same area and often as many as 20 *Batrachoseps* have been observed at one time in the beam of a flashlight. While it appeared that no salamander occupied an area to the exclusion of other salamanders, competition for food and shelter can occur without aggressive behavior and may exclude the weaker or slower animals.

Reproduction

Stebbins (1951) and Hilton (1945) have described females possessing eggs. Davis (1952) described the eggs and larvae of *B. pacificus* for the first time in detail. No eggs of *B. pacificus* were discovered during the study despite many thorough searches of the study plot. Apparently the eggs were deposited underground and, even during the week of January 22-28, when nearly 8 inches of rain fell there was no indication of eggs having been brought to the surface. Many apparently recently hatched individuals were discovered, however. Groups of 3 to 12 such individuals, measuring 21 to 23 mm (total length), were discovered on January 20 and February 1 at different localities. The coloration of these salamanders matched closely the description of recently hatched *B. pacificus* larvae given by Davis (1952) and Stebbins (1951). All had dark venters with scattered guanophores laterally. A brick-red, mid-dorsal strips was laterally bordered by a solid dark band. Their coloration was mostly darker than that of the adults and they possessed a more contrasting dorsal stripe.

All recently hatched individuals were discovered in groups near a burrow at night. Apparently they exhibited the same behavior that characterizes the adults and retreated to a subterranean position during the day as none could be found in the vicinity diurnally. With very slight provocation young salamanders would respond with their characteristic "snap coils."

On March 1, four individuals collected had body and tail lengths, respectively, of 15-15 mm, 16-13 mm, 13-7 mm (apparently the tail had recently been lost), and 18-16 mm.

Behavior

Cunningham (1955) reported that *B. attenuatus* is frequently found as high as 7 feet above the ground between the loose bark and trunk of dead live oaks (*Quercus agrifolia*). This climbing proclivity is especially striking during or immediately following the early fall rains. On numerous occasions scansorial behavior was also noted in *pacificus*. Usually salamanders were discovered climbing in ivy vines or other vegetation 2 feet or less above the ground.

When handled roughly, *Batrachoseps* will move quickly and haphazardly by lashing its body from side to side in violent contortions. This behavior seems more characteristic of adult *B. attenuatus* than of adult *B. pacificus*. The young of both species seem to utilize this defensive behavior more frequently than do the adults. On other occasions when frightened they roll themselves into a tight ball and frequently a small quantity of water is emitted from the cloaca. Whenever possible *B. pacificus* will attempt to encircle an object such as a twig and they are then difficult to capture. The tail is often used in a prehensile manner and a salamander can hang for some time from a twig or vine solely by its tail. Such behavior seems more characteristic of *B. pacificus* than of *B. attenuatus*.

A deep ruby-red eyeshine was noted on several occasions with *pacificus*.

Predators

Enemies appears to be few. The ring-necked snake (*Diadophis amabilis*) which feeds primarily upon slender salamanders is more often a predator on *B. attenuatus* than on *B. pacificus*. Cunningham (1956) reported that *B. attenuatus* were frequently eaten by captive San Diego alligator lizards (*Gerrhonotus multicarinatus webbi*) with seemingly no ill effects on the lizard, although most other amphibians were rejected. In captivity, juvenile Hammond's garter snake (*Thamnophis elegans hammondi*) and the California king snake (*Lampropeltis getulus californae*) have eaten *Batrachoseps* and died soon afterward, presumably from the effects of the dermal toxins.

A case was reported to the writer of *Batrachoseps* being substituted for earthworms in the diet of a captive juvenile mockingbird (*Mimus polyglottos leucopterous*). The bird died within an hour.

Jerusalem crickets (*Stenopelmatus*) are frequently found under shelter utilized by *Batrachoseps*. Many salamanders have been found with badly mutilated tails and limbs, possibly attributable to *Stenopelmatus*. Stebbins (1954) records a case of a Jerusalem cricket consuming a *Batrachoseps* confined with it. Other animals recorded by Stebbins as being predators upon slender salamanders were the arboreal salamander

(*Aneides lugubris*), sharp-tailed snake (*Contia tenuis*), and the white-footed mouse (*Peromyscus*).

Food Habits

No stomach analyses were made but several field observations are of interest. A large *pacificus* was observed to pull an earthworm toward it with its tongue and then to consume it. On several other occasions salamanders were found in the process of eating various kinds of annelid worms. An adult *Batrachoseps* took 20 minutes to complete swallowing a worm 3 inches long. Another large individual was noted eating an earwig (Dermaptera). The most frequent food item appeared to be the sow bug (Crustacea). The salamander would seldom release its hold of the sow bug even though carried into the lighted room, marked or identified, and returned to its original sight. The process of swallowing a sow bug usually took a half hour or more.

Summary

A study of the Pacific slender salamander, *Batrachoseps pacificus* (Cope), was made in a residential lot in Santa Monica, California. To study movement and growth, 539 salamanders were marked by excising toes. The average number of salamanders found on each of nearly 100 visits was 22.

Batrachoseps are photophobic to strong illumination.

The body temperature of *Batrachoseps* approximates the soil with which the animals are in contact. Salamanders were discovered on soil between 4°-21° C. *Batrachoseps* probably derives most of its heat from the substratum.

Moisture appears to have the most limiting effect on activity. The average body water of *Batrachoseps* was 80.6%. Salamanders could withstand an average loss of body water of 34.7% without harmful effects. Small salamanders reached their vital limit faster than did larger specimens. The average water loss tolerated under normal condtions was 5.8%.

The larger the salamander, the greater the distances traversed. Of 375 salamanders recaptured at least once, 92% changed cover, many moving over 3 feet. Some individuals left their usual range to establish a new home range. Most cases of changed ranges seem attributable to man-induced habitat alterations. The size and shape of the home range are dependent upon the microenvironment. *Batrachoseps* occasionally make extended excursions of short duration outside their range. Some individuals appeared to be transients moving through the study area. The average maximum distance of capture for 141 salamanders captured at least 5 times was 19.8 feet.

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THE DISTRIBUTION OF SMALL MAMMALS IN RELATION TO THE CLIMAX VEGETATION MOSAIC IN EASTERN WASHINGTON AND NORTHERN IDAHO[1]

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Introduction

Animals are but part of a complex unit, the ecosystem, containing also plants, edaphic factors, and climatic factors. Wherever equivalent combinations of edaphic and climatic factors occur over the landscape a characteristic climax vegetation, or its seral precursors, provides a basis for the recognition of ecosystems. As the vegetation pattern varies, altering the food and shelter conditions for animals, it has often been shown that there are also corresponding variations in the animal components of the ecosystems.

The purpose of this investigation was to sample quantitatively the small mammal component, primarily mice and shrews, of various ecosystems as indicated by climax plant associations and to relate the distribution of small mammals to the vegetation mosaic. Previous workers have shown that the designation of mammalian habitats in terms of vegetation units facilitates comparisons of the sampling sites as to floristic composition as well as physiognomy and phenology, all of which are of importance concerning the nutrition and shelter requirements for small mammals. However, the degree of refinement that is both practical and useful has not been established.

A classification of the vegetation of the study area has been presented by Daubenmire (1942, 1952), and systematic treatments of the small mammals have been presented by Davis (1939), Dalquest (1948), and Booth (1947). Although there have been studies concerned with the ecological distribution of small mammals in this area, *e.g.* Dice (1916) and Larrison (1944), as far as is known, there have been no published studies relating the distribution of small mammals to specific climax associations.

The Study Area

Location

The study area, including semidesert, grassland and forest, lies east of the Big Bend of the Columbia River in Washington, west of the main mass of the Bitterroot Mountains, and just north of the east-west line formed by the Snake and Clearwater Rivers. Twenty-four stands selected to represent fourteen climax plant associations were distributed over Whitman, Adams, and Spokane Counties in eastern Washington, and Latah and Shoshone Counties in adjacent Idaho (See Figure 1). In elevation the stands range from about 427 meters in the vicinity of Lacrosse, Whitman County, Washington, to 1,784 meters at Freezeout Saddle in the Bitterroot Mountains of Shoshone County, Idaho.

Vegetation

Vegetation is termed climax when there is no concrete evidence that in the absence of disturbance it is followed by a different plant community. The term climatic climax is applied to that type of vegetation equilibrium which is characteristic of undulating topography and moderately drained loamy soils, while the term topographic climax is applied to the vegetation that differs from the climatic climax as a result of microclimates differentiated by topography. Wherever strong soil peculiarities accompany steep topography, the term topoedaphic climax is used.

The basic unit of vegetation classification is the association, and the smallest unit of vegetation is the union. The union is charatcerized by a species or group of species closely similar in micro-environmental requirements. The association then is composed of all the plant unions intermingled on the same area. Each distinctive combination of unions is ordinarily considered a separate association, which is represented in the field by numerous stands.

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A vegetation zone is characterized by a distinctive climatic climax plant association which forms the matrix vegetation over the extent of the zone and enmeshes stands of topographic and/or topoedaphic climax vegetation. Climax vegetation is therefore regarded as a mosaic of associations differentiated by soil and climate.

The native vegetation of the study area has been greatly modified by the activities of man. Although most of the non-forested area is devoted to agriculture, small areas may be found that are relatively undisturbed. However, there is little assurance that any of the areas used in this study will remain undisturbed for very long.

The non-forested region may be subdivided into 3 vegetation zones (Figure 1), each characterized by a distinctive climatic climax association. These zones, arranged according to increasing precipitation and decreasing temperature, are (1) *Artemisia* semi-desert zone, (2) the *Agropyron* grassland zone, and (3) the *Festuca* grassland zone. The forested region is subdivided into 4 vegetation zones arranged in similar sequence as above being (1) *Pinus ponderosa* zone, (2) *Pseudotsuga menziesii* zone, (3) *Thuja plicata-Tsuga heterophylla* zone, and (4) *Picea engelmannii-Abies lasiocarpa* zone.

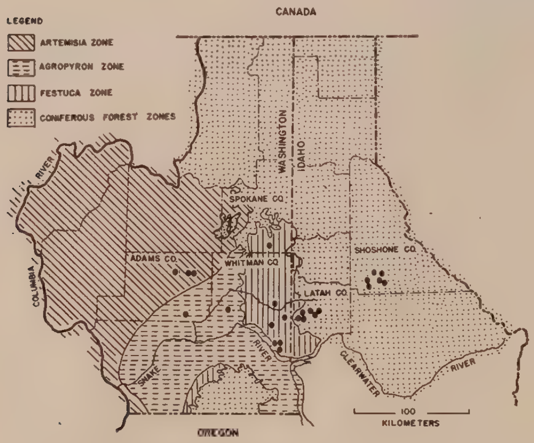

FIG. 1. Distribution of study sites in relation to major vegetation units.

The plant associations studied in these zones may be characterized briefly as follows:

(1) The *Artemisia/Agropyron* association—Stands of this association form the characteristic climatic climax vegetation of the *Artemisia* semi-desert zone. The large, perennial, evergreen shrub *Artemisia tridentata* dominates the physiognomy of each stand and comprises the *Artemisia* union. The *Agropyron* union is subordinate and consists of tall perennial bunch grasses such as *Agropyron spicatum* and *Festuca idahoensis*. *Balsamorhiza sagittata*, and other perennial forbs, may be locally abundant but grasses are the principal herbs. The *Poa* union is subordinate to the *Agropyron* union and consists of *Poa secunda* as well as other small perennials such as *Antennaria dimorpha* and *Lomatium macrocarpum*, together with small annuals such as *Draba verna*, *Collinsia tenella*, *Plantago purshii*, and *Stellaria nitens*. These plants of the *Poa* union all dry earlier in the season than the larger vascular plants. The *Chrysothamnus* union consists of *Chrysothamnus nauseosus* and *C. viscidiflorus*. These are low shrubs widely scattered among the other plant unions. In all, then, 4 vascular plant unions comprise the *Artemisia/Agropyron* association.

(2) *The Artemisia rigida/Poa* association—Stands representative of this association are dominated by the small shrub *Artemisia rigida* which comprises the *Artemisia rigida* union. These shrubs are widely spaced, and the *Poa* union occupies the intervening spaces. Stands of this association occur as edaphic climaxes along the brows of hills on thin, stony soils within the *Artemisia* and the *Agropyron* zones.

(3) The *Agropyron/Poa* association—Stands of this association form the characteristic climatic climax vegetation of the *Agropyron* grassland zone. The *Agropyron* union dominates the physiognomy of each stand and gives the vegetation its characteristic bunchy appearance when viewed from a distance. The *Poa* union is subordinate. The *Chrysothamnus* union is a constituent of stands as climatic climax vegetation, but is absent from stands that occur as topographic or topoedaphic climaxes on steep southward facing slopes within the *Festuca* grassland zone.

(4) The *Festuca/Symphoricarpos* association—Stands of this association form the characteristic climatic climax vegetation of the *Festuca* grassland zone. The *Festuca* union is dominated by the grasses *Festuca idahoensis* and *Agropyron spicatum* with a rich assortment of forbs such as *Helianthella douglasii*, *Balsamorhiza sagittata*, *Heiracium albertinum*, and *Lupinus sericeus*. The *Symphoricarpos* union consists of deciduous shrubs primarily *Symphoricarpos rivularis*, *Rosa ultramontana*, *R. spaldingii*, and *Prunus virginiana* var.

melanocarpa. These shrubs are strongly dwarfed, attaining a height at maturity less than that of the grasses and forbs. The *Poa* union is absent. Stands of the *Festuca/Symphoricarpos* association lack the characteristic bunchy appearance of the *Agropyron/Poa* association and instead present a more or less evenly dense sward when viewed from a distance.

(5) The *Symphoricarpos/Festuca* association —The unions comprising this association are the same as described in the preceding association. However, the order of dominance is reversed. Shrubs dominate the vegetative physiognomy and form dense thickets ranging from one-half to about one meter in height. The *Festuca* union is subordinate. Small scattered stands occur as topographic climaxes on north-facing slopes and protected sites on upland slopes within the *Festuca* grassland zone.

(6) The *Crataegus/Symphoricarpos* association —Stands of this association occur as topographic climaxes along steep slopes that appear to have an above-average moisture balance in the *Festuca* grassland zone. The *Crataegus* union is composed of small deciduous trees such as *Crataegus douglasii, Populus tremuloides, Prunus virginiana* var. *melanocarpa,* and *Amelanchier alnifolia,* forming a more or less continuous canopy. The *Symphoricarpos* union is subordinate. The height of the shrub union is increased in this association but its coverage is much reduced. The herbaceous vegetation is derived largely from the *Festuca* union.

(7) The *Pinus/Symphoricarpos* association— Sands of this association form the characteristic climatic climax vegetation in the region where the *Pinus ponderosa* zone occurs adjacent to the *Festuca* grassland zone. Some stands also occur as topographic climaxes on relatively moist sites within the *Festuca* grassland zone. The *Pinus* union consists of the single tree species, *Pinus ponderosa*. The *Symphoricarpos* union is subordinate. The herbs accompanying the *Symphoricarpos* union are a mixture of species derived from the *Festuca* grassland zone plus others confined to coniferous forests.

(8) The *Pinus/Physocarpus* association— Stands representing this association occurs as topographic climaxes on sites adjacent to stands of the *Pinus/Symphoricarpos* association where the moisture balance is higher. *Pinus ponderosa* comprises the *Pinus* union. The *Physocarpus* union is dominated by deciduous shrubs forming a dense canopy about 2 meters tall. *Physocarpus malvaceus* is usually most abundant, with lesser amounts of *Holodiscus discolor, Ceanothus sanguineus,* and *Philadelphus lewisii.* The *Physocarpus* union is accompanied by the *Symphoricarpos* union. The herbaceous vegetation is represented by still fewer grassland species mingled with herbs characteristic of the forests.

(9) The *Pseudotsuga/Physocarpus* association —Stands representing this association occupy relatively little area as climatic climax but are extensive as topographic climaxes on northward facing slopes and ravines within the *Pinus ponderosa* zone. The *Pseudotsuga* union is comprised of the single tree species *Pseudotsuga menziesii*. The subordinate shrub unions are the same as described for the preceding association. However, the shrub unions tend to be suppressed in height and tend to be greatly reduced in coverage in the climax stands studied.

(10) The *Thuja/Pachistima* association— Stands of this association occur as climatic climax in the southern extension of the *Tsuga heterophylla-Thuja plicata* zone, on habitats where moisture relations are more favorable than those of the previously described association. The *Thuja* union is comprised of *Thuja plicata* often with a few individuals of *Abies grandis* present. The *Pachistima* union is subordinate and consists of a complex but distinctive array of forbs and a few shrubs of widely different life forms. Representative species of the *Pachistima* union are *Pachistima myrsinites, Coptis occidentalis, Asarum caudatum, Athyrium filix-foemina, Linnea borealis* var. *americana, Actaea arguta, Adenocaulon bicolor, Mitella stauropetala, Smilicina stellata, Trillium ovatum, Viola glabella, Rosa gymnocarpa,* and *Taxus brevifolia.*

(11) The *Picea-Abies/Pachistima* association —Stands of this association occupy the lower part of the *Picea-Abies* zone where it appears to be climatic climax. As topographic climax it extends to lower elevations. The *Picea-Abies* union is typically comprised of various mixtures of *Picea engelmannii* and *Abies lasiocarpa,* although the stand studied on Moscow Mountain lacks this species of *Abies* entirely. The *Pachistima* union forms the undergrowth.

(12) *Picea-Abies/Xerophyllum* association— Stands of this association occupy the higher parts of the *Picea-Abies* zone where they occur as topographic climaxes on steep southward facing slopes. The *Picea-Abies* union may be locally supplemented or replaced by *Tsuga mertensiana.* The *Xerophyllum* union is comprised almost entirely of but 2 species, *Xerophyllum tenax* and *Vaccinium membranaceum.*

(13) *Picea-Abies/Menziesia* association—The stands studied are not regarded as typical of the

association in general as they have in addition to the *Menziesia* and *Xerophyllum* unions a fair represenatation of the *Pachistima* union. The understory is dominated by the *Menziesia* union presenting a brushy physiognomy to about 1.5 meters in height composed primarily of *Menziesia ferruginea.* The stands thus represent an intergrade between the typical *Menziesia* and typical *Pachistima* associations.

(14) The *Festuca viridula* association—Stands of this association occupy steep south facing slopes as topoedaphic climaxes in the *Picea-Abies* zone. The tall perennial bunch grass *Festuca viridula* is dominant. Characteristically these stands lack *Xerophyllum tenax* and *Vaccinium membranaceum* common to the forest association on the same slopes.

Materials and Methods

Stands were selected for study on the basis of their floristic composition and relative freedom from the visible effects of man-caused disturbances. One association was represented by 3 stands, 8 associations were represented by duplicate stands, and 5 associations were represented but once. Most of these stands varied in size from less than an acre to many acres; however, a few were not much larger than the 16 x 32 meter dimensions of the trapping area used. A constant area size was used in all stands to justify the comparison of trapping results. A trapping area consisted of 3 lines of 5 stakes each with lines and stakes spaced 8 meters apart. Forty-five snap-traps of the type commonly sold as "mouse traps" were set in each stand, 3 of these being grouped and confined to a one meter radius about each stake. A mixture of oatmeal and peanut butter was used as bait, although a few trials were made using fresh carrot root in an unsuccessful attempt to attract *Lagurus.* A trapping period usually consisted of 3 consecutive days, although in a few instances only 2 consecutive days are recorded, and in one instance a period is represented by only one day. Most of the sites were trapped at least twice during 1954 and 3 times in 1955 with trapping periods approximately one month apart. Four of the stands were trapped only in 1955. Trapping results are computed using the catch per trap-day method.

The percentage of full sunlight reaching the ground through the vegetative canopy was used as a measure of the density and arrangement of the vegetation available as cover for small mammals. Light intensity measurements were made using a Weston Model 756 sunlight illumination meter. These measurements were usually made on sunny days without cloud interference and near mid-day. The photosensitive element was covered with a semicylindrical translucent plastic hood to integrate some side light with that coming from directly above the sensitive cell. The procedure involved the placement of a tape along the ground, then making light-meter readings at 2-decimeter intervals along the tape. Measurements of full sunlight intensities were made above the vegetative canopy. The photosensitive element was then placed on the ground alongside the tape-line at a designated point and a second light reading was obtained and recorded. This procedure was repeated at 2-decimeter intervals until 50 readings were made along 10 meters of tape. The percentage of full sunlight reaching the ground through the vegetative canopy was then computed. This procedure proved satisfactory for grassland and shrubby physiognomies where measurements of full sunlight could be obtained without interference from tree canopies.

Results and Discussion

The results of this investigation are presented in Table I. Six-hundred small mammals were trapped during 14,175 trap-days. Two orders of small mammals are represented in the trapping results, Insectivora and Rodentia. The insectivores are represented by a single family, Soricidae, and by 3 species of the genus *Sorex*— *S. vagrans* (Baird), *S. cinereus* (Kerr) and *S. obscurus* (Merriam). The rodents are represented by 3 families—Sciuridae, Heteromyidae, and Cricetidae. The Sciuridae is represented by *Eutamias amoenus* (Allen), the Heteromyidae by *Perognathus parvus* (Peale) and the Cricetidae by *Lagurus curtatus* (Taylor), *Microtus montanus* Peale, *M. longicaudus* (Merriam), *Clethrionomys gapperi* (Rhoads), *Reithrodontomys megalotis* (Baird) and *Peromyscus maniculatus* (Wagner).

Peromyscus maniculatus was trapped in nearly every stand sampled and comprised over 50% of the total catch (Table I).

The distribution of small mammals is presented in relation to their presence in the various vegetation zones.

Small Mammals of the Artemisia *and* Agropyron *Zones*

Four species are represented in the 5 stands sampled in the *Artemisia* and *Agropyron* vegetation zones (Table I). These are *Lagurus curtatus, Perognathus parvus, Reithrodontomys megalotis* and *Peromyscus maniculatus.* Only *Lagurus* and *Perognathus* appear to be restricted

TABLE I. The distribution of small mammals trapped in relation to climax plant associations in eastern Washington and adjacent northern Idaho, the stands are arranged along the altitudinal gradient from low to high elevations

Zone	Stand	Trap-days	*L.c.*	*P.p.*	*R.m.*	*P.m.*	*M.m.*	*M.l.*	*S.v.*	*E.a.*	*C.g.*	*S.c.*	*S.o.*	Total
Artemisia	1. *Artemisia rigida/Poa*	675	1	14		11								26
	2. *Artemisia tridentata/Agropyron*	675	1	16	3	19								39
	3. " " "	675		32		31								63
Agropyron	4. *Artemisia rigida/Poa*	675		5		22								27
	5. *Agropyron/Poa*	675		24		11								35
Festuca	6. " "	675				25								25
	7. " "	675			2	30		1						33
	8. *Festuca/Symphoricarpos*	540					8	2	1					11
	9. " "	180				3								3
	10. *Symphoricarpos/Festuca*	540			1	17		55	1					74
	11. *Crataegus/Symphoricarpos*	540				1		1						2
	12. *Pinus/Symphoricarpos*	540				20		9	3	5				37
Pinus ponderosa	13. " "	675				9		1		5				15
	14. *Pinus/Physocarpos*	675				6		2	1	6	5			20
	15. *Pseudotsuga/Physocarpus*	675				8		1		8	4			21
Pseudotsuga	16. " "	675				3			5	3	2			13
Thuja—Tsuga	17. *Thuja/Pachistima*	675				15				4	11	5		35
	18. *Picea—Abies/Pachistima*	630				5			1	*	2	2		10
Picea—Abies	19. *Picea—Abies/Menziesia*	630				12			2	4	5	6	3	32
	20. " " "	450				18			1	*	1			20
	21. *Picea—Abies/Xerophyllum*	630				9				3	4	2		18
	22. " " "	360				6				*	2	1		9
	23. *Festuca viridula*	585				15								15
	24. " "	450				17		1						18
	Totals........	14,175	2	91	6	313	8	73	15	38	36	16	3	601

L.c. = *Lagurus curtatus*
P.p. = *Perognathus parvus*
R.m. = *Reithrodontomys megalotis*
P.m. = *Peromyscus maniculatus*
M.m. = *Microtus montanus*
M.l. = *Microtus longicaudus*
S.v. = *Sorex vagrans*
E.a. = *Eutamias amoenus*
C.g. = *Clethrionomys gapperi*
S.c. = *Sorex cinereus*
S.o. = *Sorex obscurus*
* = *observed but not trapped*

in distribution to these 2 vegetation zones (Figure 2).

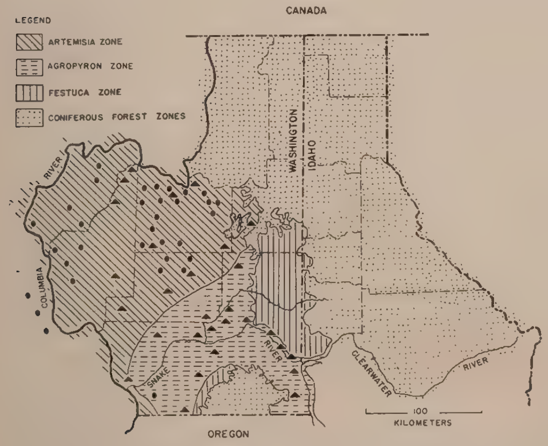

FIG. 2. Distribution of *Lagurus* (dots) and *Perognathus* (triangles) in relation to the *Artemisia* and *Agropyron* zones (museum records).

Lagurus was trapped only in the stands sampled in the *Artemisia* zone. The predilection of *Lagurus* for Big Sagebrush is well known and the close agreement between the distribution of Big Sagebrush and *Lagurus* in eastern Washington is illustrated in Figure 2. The distribution of *Lagurus* appears to be related in some way to the occurrence of Big Sagebrush as it apparently does not occur in the *Agropyron* zone which consists essentially of the same vegetative but lacks the *Artemisia* union. It is known that *Lagurus* feeds upon the leaves of Big Sagebrush (James and Booth 1954) and this evergreen shrub may also serve as a source of water especially in late summer and early autumn when plants of the herbaceous unions are dry and when there may be prolonged periods without precipitation. The apparent absence of *Lagurus* from the *Agropyron* zone suggests that water relations are more limiting for certain microtines in the *Agropyron* zone than in the *Artemisia* zone although the latter receives less annual precipitation (Daubenmire 1956).

Lagurus populations are subject to extreme fluctuation. At times they may be abundant and then suddenly almost disappear (Moore 1943). They do not accept baits readily (Johnson *et al.* 1948). It seems likely that a low population and poor bait acceptance has contributed to the paucity of the *Lagurus* catch.

Perognathus parvus is represented in both the *Artemisia* and *Agropyron* zones but it apparently does not extend into the *Festuca* zone. The factors responsible for the distribution of *Perognathus* into the *Agropyron* zone and for the failure of *Lagurus* to extend its distribution into this zone are not known with certainty. However, it is well known that the water requirements of *Perognathus* are low (Schmidt-Nielsen *et al.* 1948) and it lives well on a diet consisting exclusively of air-dry foods. The predilection of *Lagurus* for succulent plant tissues has also been reported (Hall 1946, p. 558). It seems likely that the ability of *Perognathus* to withstand very dry conditions is at least in part responsible for its distribution in the *Agropyron* zone. In the climatic climax vegetation of the *Agropyron* zone *Peroganthus* appears to be the best represented small mammal (Table I, Stand 5).

The apparent absence of *Perognathus* from the *Festuca* zone does not appear to be related to vegetation *per se* since it did not occur in stands of the *Agropyron/Poa* association which occur as topographic or topoedaphic climax vegetation within the *Festuca* zone. These stands have essentially the same vegetative composition as climatic climax stands. Two features of the *Festuca* zone aside from matrix vegetation distinguishing it from the *Artemisia* and *Agropyron* zones are the greater annual precipitation (Daubenmire 1956) and the heavy-textured soils (Lotspeich and Smith 1953).

The predilection of *Perognathus* for sandy-textured soils is well known (Hall 1946, p. 49). The soils of the *Artemisia* and *Agropyron* zones have a high percentage of sand in the profile into which *Perognathus* readily burrows, sometimes to depths of 6 feet (Scheffer 1938). The heavy-textured soils of the *Festuca* zone become hard upon drying and could conceivably discourage the deep burrowing of *Perognathus*. Soils supporting stands of the *Agropyron/Poa* association as topoedaphic climax vegetation consist of this same kind of heavy textured material intermixed with large amounts of basaltic stones. Moisture penetrates deeply and may also contribute to an unfavorable burrowing environment for *Perognathus*.

The small stands representing the *Artemisia rigida/Poa* association as topoedaphic climax vegetation within the matrix climatic climax vegetation of the *Artemisia* and *Agropyron* zones do not appear to have a characteristic small mammal species-composition of their own but take on the composition of the surrounding matrix vegetation.

Small Mammals of the Festuca *Zone*

From these samples, only one small mammal, *Microtus montanus,* appears to be restricted in distribution to the climax vegetation of the *Festuca* zone. Other species trapped within this zone occur in other vegetation zones. Only *Peromyscus maniculatus* and *Reithrodontomys megalotis* appear in more xeric zones while *Microtus longicaudus, Sorex vagrans* and *Eutamias amoenus* are trapped here and also in the more mesic coniferous forest zones.

The comparatively low and erratic catch of *Microtus montanus* (Stands 8 and 9) suggests that the climatic climax stands of the *Festuca/Symphoricarpos* association provide only the minimum environmental requirements for this mouse since it is commonly found in hay and alfalfa fields as well as certain other kinds of dense herbaceous vegetation in eastern Washington (Larrison 1944). The dominance of the herbaceous *Festuca* union provides a habitat that yields a rather low trap success whereas a dominance of the shrubby *Symphoricarpos* union provides a habitat that yields high trap success (Stand 10) particularly of *Microtus longicaudus*. Where the *Symphoricarpos* union is suppressed by the imposition of tree unions the catch of *M. longicaudus* is reduced. There appears to be a rather close relationship between the distribution of the *Symphoricarpos union* and the occurrence of *M. longicaudus* (Stands 8, 10, 11, 12, 13, 14 and 15).

Reithrodontomys megalotis and *Sorex vagrans* are poorly represented in the trapping results from the *Festuca* zone. *Sorex vagrans* appears to reach its lower (xeric) phytosociologic limits in the *Festuca/Symphoricarpos* association. Little information concerning distribution is derived from the paucity and erratic distribution of the catch of *Reithrodontomys megalotis,* however, it did not occur in any of the stands sampled in the coniferous forest. Seral vegetation of the weedy annual type rather than climax vegetation seems to be the preferred habitat of this mouse (Hardy 1945)

An evaluation of the influence of vegetation cover upon the local distribution of mice was made in three contiguous stands of vegetation representative of the *Festuca* zone. The study area consists of about 28 acres of relatively undisturbed vegetation (Johnsgard and Rickard 1957) and is comprised of 3 plant associations—*Agro-*

pyron/Poa, Festuca/Symphoricarpos and *Symphoricarpos/Festuca* (Stands 7, 8 and 10).

Microtus montanus is restricted in distribution to the *Festuca/Symphoricarpos* association. *M. longicaudus* is most frequently trapped in the *Symphoricarpos/Festuca* association although occasionally occurring in the other 2 associations. *Peromyscus maniculatus* is most frequently trapped in the *Agropyron/Poa* association although it is rather frequently represented in the *Symphoricarpos/Festuca* association as well.

The amount and kind of vegetative cover provided by each stand appears to be an important factor in the local distribution of certain mice. As a criterion of the amount of vegetative cover provided by each stand the percentage of full sunlight intercepted by the vegetative canopy was measured in each stands. The results are presented in Figure 3. The *Agropyron/Poa* stand provided the smallest amount of canopy coverage while stands of the *Festuca/Symphoricarpos* and *Symphoricarpos/Festuca* association were both high in canopy coverage but yielded somewhat similar light measurement values. Although the measured canopy coverage values are similar for these latter 2 stands each provides a distinctive habitat for small mammals. The close spacing of grasses and forbs in the *Festuca/Symphoricarpos* association allows the construction of runways while the paucity of a herbaceous understory and the spacing of woody stems in the *Symphoricarpos/Festuca* association precludes the possibility of runway construction.

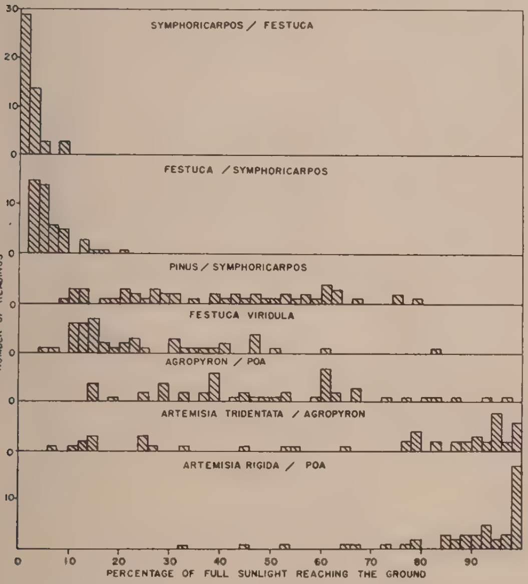

FIG. 3. Vegetative cover provided by certain stands as determined by light meter measurements.

Microtus montanus characteristically constructs runways while *M. longicaudus* apparently does not (Booth 1947). This difference in behaviour may, at least in part, be responsible for the more or less separate distribution of these microtines.

The presence or absence of a dense vegetative canopy appears not to be of primary concern in the distribution of *Peromyscus*. It occurs in stands of high and low canopy coverage; however, it did not occur in the stand of the *Festuca/Symphoricarpos* association which offers the most vegetative resistance to movement along the ground surface. *Peromyscus* and *Perognathus* are both characteristic mammals in stands of low vegetative coverage (Figure 3). Apparently these nocturnal mammals rely less upon vegetation as protection from predators than do most of the diurnal microtines.

While the topoedaphic climax stands of vegetation within the *Artemisia* and *Agropyron* zones appear to take on the species composition of the surrounding matrix vegetation such stands in the *Festuca* zone appear to have their own species composition.

Small Mammals of the Coniferous Forest Zones

Four species were trapped only in coniferous forest stands. These were *Eutamias amoenus, Clethrionomys gapperi, Sorex cinereus* and *Sorex obscurus.*

Eutamias was trapped or observed in every forest stand sampled even occurring in an isolated stand of the *Pinus/Symphoricarpos* association within the *Festuca* zone (Table I, Stand 13).

Clethrionomys was represented throughout the coniferous forest but was not trapped at the lower (xeric) edge of the forest (Stand 12). The absence of *Clethrionomys* from the more xeric forest stands has also been reported by Booth (1947). Apparently *Clethrionomys* does not occur in isolated forest stands within the *Festuca* zone (Svihla and Svihla 1940).

Sorex vagrans appears to attain its upper phytosociologic limits at the upper edge of the extent of the *Pachistima* union (Stands 19 and 20) while *Sorex cinereus* appears to attain its lower phytosociologic limits at the lower limits of the *Pachistima* union (Stand 17). *Sorex obscurus* was seldom trapped and was taken only in a single stand (Stand 19).

The distribution of *Eutamias* corresponds closely to the extent of the coniferous tree unions. *Eutamias* is the most arboreal of the small mammals trapped. *Clethrionomys* is not so closely related to the distribution of tree unions as is *Eutamias* but appears to be more frequently trapped in the more dense portions of the understory vegetation, particularly near fallen logs. The distribution of carnivorous *Sorex* spp. does not appear to be as directly related to the distribution of plant unions as are the distributions of the more herbivorous small mammals. The *Peromyscus* distribution extends throughout the coniferous forest and into isolated stands of the *Festuca viridula* association at the upper limits of the coniferous forest. These grassland stands do not appear to take on the species of the coniferous forest but take on a small mammal species composition of their own comprised mainly of *Peromyscus* (Stands 23 and 24). The physiognomy of these stands is similar to that of *Agropyron/Poa* stands in the *Festuca* zone and the preponderance of *Peromyscus* is simliar in both.

Two species representative of the coniferous forest were not trapped in any of the stands sampled. These were *Phenacomys intermedius* and *Zapus princeps*. It seems likely that these small mammals are represented in certain stands not sampled in this investigation.

House mice (*Mus musculus*) were not trapped in any of the stands sampled which is probably indicative of the undisturbed vegetation comprising each stand.

SUMMARY

Twenty-four stands representative of 14 relatively undisturbed climax plant associations in eastern Washington and northern Idaho were sampled for their small mammal species composition during the summers of 1954 and 1955. The same bait, number and arrangement of traps was used in each stand to facilitate the comparison of trap results.

Six hundred small mammals representing 11 species were trapped during 14,175 trap-days. The distribution of each species is discussed in relation to occurrences in the stands sampled. The definition of plant associations as particular combinations of unions is useful for expressing the variations in floristic composition and physiognomy which contribute to the vegetation requirements of small mammals.

ACKNOWLEDGMENTS

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SOME ASPECTS OF THE BEHAVIOR AND OF THE TERRITORY OF A DENDROBATID FROG, *PROSTHERAPIS TRINITATIS*

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INTRODUCTION

Territoriality, the defense of an area by one or more individuals against the invasion of that area by other members of the same species, has been observed in some arthropods and in many vertebrates. However, it was not until recent years that active territorial defense was reported for amphibians. Test (1954) observed that females of the South American dendrobatid frog, *Prostherapis trinitatis,* defended areas against invasion by other frogs of the same species. Test also described some aspects of the territorial behavior of the frogs. Martof (1953) previously had demonstrated that male green frogs, *Rana clamitans,* maintained the same spatial relationships to each other within the calling congress even though the group moved considerable distances. He suggested that this was evidence of a weak territoriality. Goin (1955) described some activities in the bull frog, *Rana catesbeiana,* which were highly suggestive of territorial defense. Grant (1955) has presented evidence interpreted as indicating territoriality in 2 species of salamanders, *Eurycea bislineata* and *Hemidactylium scutatum.* Stebbins and Hendrickson (1959) believe that the guarding of the eggs by male *Phyllobates punctatus* is another example of territorial behavior.

Further studies of the ethology and natural history of *Prostherapis trinitatis* were undertaken at the Estación Biológica de Rancho Grande, located in the Parque Nacional Henry Pittier, Estado Aragua, Venezuela, from June 20 until September 3, 1956. The main purpose of this investigation was to determine the physical nature of the structural features making up the territorial area.

LOCATION AND DESCRIPTION OF THE AREA

The study was undertaken at several localities in the Parque Nacional Henry Pittier, maintained by the Venezuelan federal government, in the coastal mountains paralleling the Caribbean Sea in the north central part of the country. Beebe and Crane (1947) have described the general area.

The Iron Bridge Area was used for both descriptive and experimental studies. This locale is on the interior side of the coastal mountains at an elevation of 3450 ft. The actual study area included a mountain stream and the adjacent rocky shores. The stream averaged 11 ft in width and 3 in. in depth during periods of non-flooding. After heavy rains the width increased to 20 ft and the depth to 18 inches. The average normal velocity of the stream was 1.6 ft/sec. Deep pools and high waterfalls were located both upstream and downstream from the study area. The stream bed and the shores were covered with stones, rocks, and boulders. The stream flowed almost directly from north to south through a ravine; the width of the ravine floor averaged 24 ft, and the slope of the walls varied from 45° to 70°. The ravine floor was exposed to the sun for about 2 hours daily during the summer, 10:30 A.M. until 12:30 P.M., and it was shaded by the ravine sides and the trees growing on them at other times. There were no trees and only a few herbs growing on the ravine floor.

The relative humidity of the area, measured with a Friez psychrometer model HA-2, varied from a low of 86% to a high of 98% during the summer. This constant high level was maintained by the neblina or fog covering the mountains during much of the day and by the rains of the summer wet season. The lowest temperature recorded by a Taylor maximum-minimum thermometer kept on the area for the entire period was 16.0°C, and the highest temperature was 20.5°C. The greatest daily variation was 3.5°C, and the least daily variation was 1.0°C.

The most common vertebrates of the area were frogs. *Prostherapis trinitatis, Atelopus cruciger,* and *Eleutherodactylus anotis* inhabited the ravine. The snakes, *Leimadophis reginae* and *Bothrops atrox,* were frequently seen. A phoebe, *Sayornis nigricans,* was the most frequently observed bird.

Two other areas were used for experimental studies. One was located on a small sand bar in the middle of a mountain stream at an elevation of 3500 ft on the interior side of the mountains. The second was along a mountain stream on the coastal side of the mountains at an elevation of 1150 ft.

METHODS

In order to correlate the movements of individual frogs with the location of the various physical features of the habitat, a base map showing the location of the shoreline and of all rocks larger than 2 in. by 2 in. was prepared. The study area mapped was a rectangle 12.5 ft by 27 ft. The long axis of the rectangle paralleled the stream, and the eastern half of the rectangle included the stream bed while the western half included one shore. The travels of individual frogs were traced on a sheet of onion skin paper placed over this base map.

The first half of the summer was devoted to a descriptive study of the animals, their behavior, and their territory. Activities such as spatial movements, territorial defense, feeding, courtship, care of the young, and others were observed from an unobtrusive site after an initial 15 minute waiting period during which the activities of the frogs returned to normal.

Subsequent to the period of observation experimental studies were carried out which were designed to check and to amplify the conclusions made on the basis of the observations. Each of the experiments was allowed to run for a period usually varying from 4 to 7 days. During these periods the experimental area was censused for a definite time, and the location, sex, size, and activities of all frogs were noted.

Observational Results

The sex and size classes and their distribution

The frogs inhabiting the study areas were divided into 3 classes: adult females, adult males, and subadults or juveniles. The adult females were readily distinguished from members of the other two classes by their greater size and by coloration and behavior. Twenty-six females from the Iron Bridge area ranged in snout-anus length from 2.1 to 2.9 cm and averaged 2.56 cm. The throat of the female is sulfur yellow bordered posteriorly by a transverse black band. The dorsum is brown, sometimes mottled with darker pigmentation. Mertens (1957) has pictured the frog so that distinguishing features are apparent, but this species was never observed in a tree by our party although it is so shown in Merten's paper. *Prostherapis trinitatis* is an inhabitant of the rocks along the shore and in the water. The female does not take care of the young. The males are smaller than the females; 8 males from the Iron Bridge Area ranged from 2.2 to 2.4 cm in length and averaged 2.31 cm. The throat of the male is not as prominently marked as is that of the female, for the yellow is less intense as is the bordering black bar. The male transports the tadpoles on his back. The subadults and juveniles are those animals with a length less than 2.1 cm. The coloration of the throat resembles that of the female. Test (1956) has described the characteristics of *Prostherapis trinitatis* in contrast to those of a closely related frog, *P. neblina*.

Members of these 3 classes were differentially distributed in the habitat. The adult females usually were located on or near rocks projecting above the surrounding substrate, either sand or water, and surrounded to varying extents by water. A census of the adults present on part of the area on July 14 revealed that 7 of the 9 adult females present in an area of 166 sq. ft were associated with rock piles in the stream while the remaining 2 were on shore. A similar census of the same area on July 27 showed that 6 of the 8 adult females present were again occupying rocks surrounded by water, and only 2 were on shore. The position of all adults on the entire area was mapped a total of 4 times. Only 6 adult females were observed on land, and the maximum distance of any of these adult female frogs from shore was 3 in.

The subadults tended to occupy areas at a greater distance from shore. A plot 11.5 ft by 12.5 ft was censused on July 19 and again on July 26. The stream bed covered 61% of the area, and the shore covered the remaining 39%. At the first census 6 subadults were on rocks within the stream and 16 were on rocks on shore. The average distance from the water's edge of animals in the latter group was 1.1 ft. The maximum distance of subadults on shore from the water was 3.7 ft. A similar census was taken on July 26, and 7 adults were observed on rocks in midstream and 8 were seen on shore. The average distance of the 8 subadults on shore from the water was 1.6 ft, and the maximum was 5.0 ft. Thus, it appears that both adult females and subadults occupy elevated structures within regions of water or sand, but that the adult females tend to occupy favorable sites near the water while the subadults disperse more widely over the shore. Typically, males do not defend territories but move about much more than individuals of the other classes. However, the few territorial males observed occupied areas similar in location to those of the adult females.

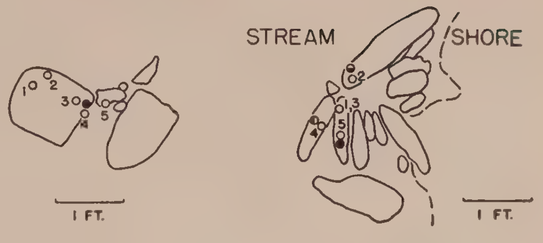
Behavior

The descriptions of the activities of the animals are based upon observations of 29 females, 13 males, and 19 subadults. Some frogs were observed more than once so that the above figures do not reflect the activities of 61 different individuals.

Test (1954) has given some description of the manner in which *Prostherapis trinitatis* defends its territory. The interaction between resident and intruder follows a definite sequence of events although some of the steps may be omitted. When the resident first observes the intruder, it orients to face the intruder. The resident's bright yellow throat is thus fully visible, and the resident pulsates the throat slowly as a challenge. Frequently, this challenge is sufficient to deter the outsider, and the intruder will move away. If this action is not sufficient, the resident may hop in the direction of the intruder and repeat the challenge. If this stimulus is still insufficient to cause the withdrawal of the invader, the resident will hop upon the back of its rival. Usually, this is the end of the encounter, and the intruder will leave the defended area. Upon certain occasions the intruder, especially if it is a large adult female, will not leave, and the resident and intruder will engage in a wrestling match. The forelimbs of each animal are extended laterally so that they project more-or-less at right angles to the long axis of the body. The hind limbs are extended so that the contestants appear to be standing. The upright position is maintained temporarily because each female is leaning against the other. While in this position each frog pushes against the other, as though to knock the opponent off balance.

This type of defense must be relatively rare and must occur only after other levels of behavior have failed to repulse the intruder, for it was only observed upon 2 occasions. One encounter lasted for 15 minutes, was broken off for 3 minutes, and then was resumed for another 7 minutes. The females struggled on top of the rocks or on the sand. Frequently, one or both of the females would fall into the water or onto the sand. The temporary loser would then hop up onto the shore or a rock in midstream and attack or be attacked. At no time was either rival hurt, and eventually the conflict ended when the larger female left the disputed area.

The adult females actively defended their territories more frequently, and were chased less frequently, than was the case for the adult males or for the subadults. Defense by adult females was observed in 11 cases of the 29 observations made of females (37.8% of the cases); adult females were chased by other frogs in only 3 of the twenty-nine cases (14.8%). The extent and location of a typical territory defended by a female is shown in Figure 1. The non-directed movements of a non-resident female are shown in Figure 2. The males were observed defending territories in only 2 of 13 instances (15.4%); they were chased in 3 of 13 cases (23.1%). The location and nature of a typical male territory is illustrated in Figure 1. Subadults defended territories in 3 instances of the 19 observations (15.8%); they were driven off by other animals in 5 cases (26.3%).



A. MALE B. FEMALE

FIG. 1. Typical territories and territorial defense by an adult male (A) and an adult female (B) *Prostherapis trinitatis*. A. The movements of the male are represented by the numbered open circles. Time at site 1, 5:15 P.M., faces intruder, a large subadult (●) but no interaction develops; 2, 5:18; 3, 5:18:30, chased intruder which moved out of area; 4, 5:22; 5, 5:24:30. Observations terminated at 5:30 P.M. B. The movements of the resident female are indicated by the numbered open circles. Time at site 1, 9:48 A.M.; 2, chased intruder ◒, a juvenal which leaves area; 3, 10:38; 4, chased large juvenal ◐; 5, 10:45 jumped and landed next to ●, another subadult, which left area. Closed continuous lines represent rocks, the dashed line the shoreline.

Territorial defense did not result in the complete elimination of trespass when an intruder was rebuffed. Frequently, the resident frog would repulse an intruder successfully only to have that same intruder return when the resident was engaged with another frog elsewhere (Figure 3). Thus, any one particular invading *P. trinitatis* may have been challenged and dominated several times within a short period.

The frogs frequently left their territories, especially when they were frightened by the investigator or by some other large moving object. Under these conditions the animals leaped into the water and swam to shelter beneath rocks out of their defended areas. The movements of a female which took refuge under a rock 5 feet outside the periphery of its territory are shown in Figure 4. Other animals which disturbed the frogs included the local phoebe, *Sayornis nigricans,* a common inhabitant of the ravines. In contrast to the reaction of the frogs to the movement of harmless animals is their reaction to motionless predators. Small fer-de-lance, *Bothrops atrox,* are commonly observed along the streams, and the frogs furnish the snakes with the major part of their diet (Sexton in press). Yet these frogs hop

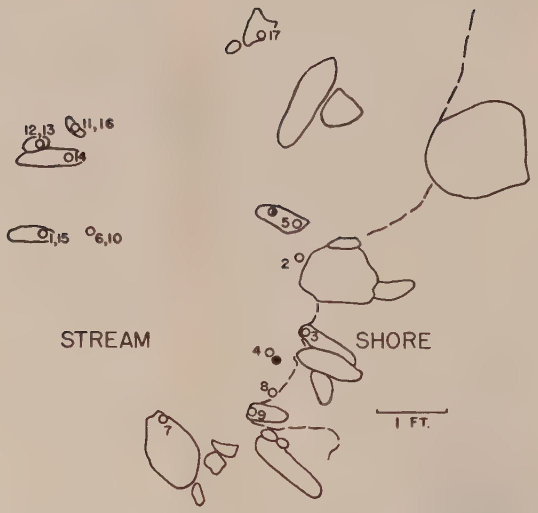


FIG. 2. Successive movements (numbered open circles) of an evidently non-resident female *Prostherapis trinitatis* chased by 2 other resident females (● and ◐). Time at site 1, 9:53 A.M.; 2, 10:02; 3, 10:03; 4, 10:05, chased from here by resident ● which jumped on intruder; 5, 10:09:30, chased by ◐ ; 6, 10:09:30; 7, 10:14, 8, 10:14:30; 9, 10:15, probably intimidated by ● again; 10, 10:19; 11, 10:19:30; 12, 10:30, temporarily lost to view behind rock; 13, 10:50; 14, 10:51; 15, 10:55; 16, 11:26; 17, 11:29. The movements of this unestablished frog are much more extensive than those of residents. Closed continuous lines represent rocks; dased line represents the shoreline.

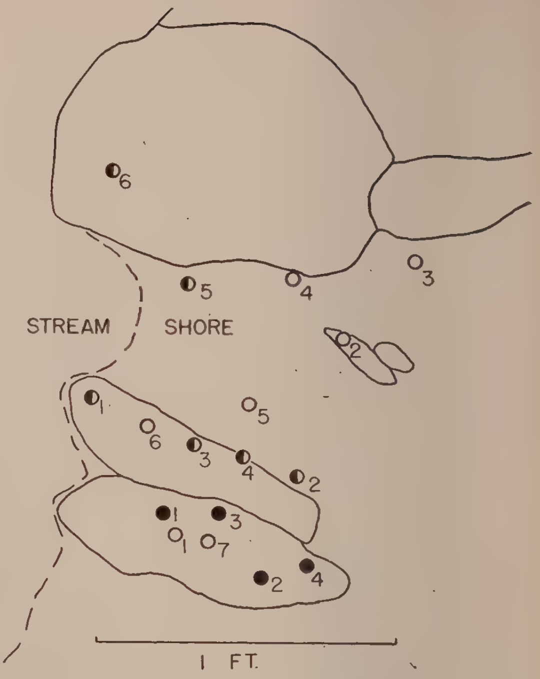


FIG. 3. The infiltration of two non-resident frogs into the area defended by a larger subadult frog. The movements of the first non-resident frog are indicated by solid circles and those of the second by half solid circles. The movements of the resident are shown by the open circles and are as follows: 1, 10:45 A.M.; resident did not disturb non-residents at ● 2 or ◐ 2; 2, 10:50, ● 3 enters area vacated by resident; 3, 10:51; 4, 10:52; 5, 10:52 residents returns and ◐ 5 and ● 4 leave; 6, 10:53; 7, 10:53.

within a few inches of the snakes when the latter are coiled up on the rocks, asleep during the day.

Other extra-territorial movements were noted during the periods of flooding. Prior to heavy flooding 7 adult females and males were observed on the study area on August 1; on the afternoon of August 2 a heavy rainstorm raised the stream level from a depth of 3 inches to one of 18 inches, flooding the entire ravine floor. Only a single male was observed in the study area on August 3 after the water level had subsided, and few *P. trinitatis* were seen in the surrounding areas. Another flood occurred August 4-5, and there were even fewer *P. trinitatis* present on the study area and adjacent areas on August 6. By August 7, five, and by August 8, eight adult females were back in the study area. Evidently, the frogs disperse during the floods, taking refuge on the ravine slopes. *Atelopus cruciger* does the same thing in the ravine (Sexton 1958).

The frogs were often seen feeding. They assumed a position on elevated structures so that they were more-or-less at right angles to a vertical drop and could look over an expanse of water and sand. From this position they would leap at small moving objects, including floating leaves as well as insects.

In the only observed instance in which more than one frog attempted to catch the same prey, a small insect, there were no observed interactions between the potential competitors. A large female and two subadults were initially attracted by an insect. The female moved toward the insect but paused. At this time a second large female leaped out of the water and in front of the other 3 frogs, engulfed the prey, and dove back into the water.

Physical nature of the territory

The location, distribution, and area of the territories occupied during any observation period was determined by plotting the movements of the animals over the base map. The perimeter of the territory was established by drawing a line

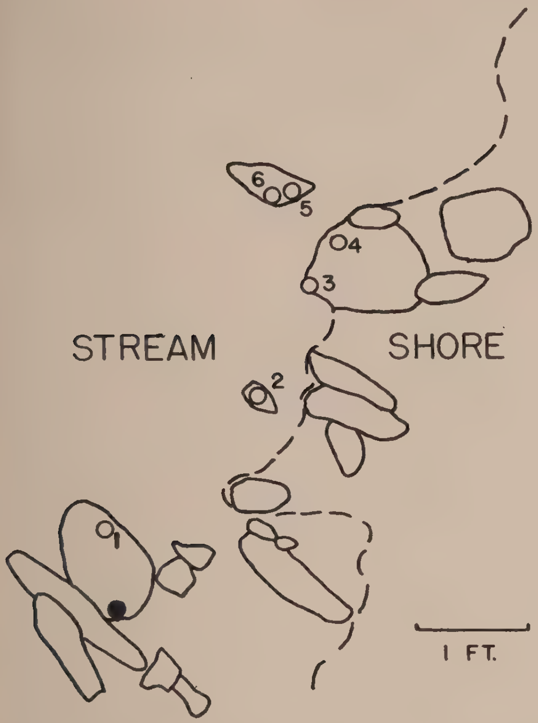


Fig. 4. The hiding place of this adult female *Prostherapis trinitatis* is outside of the female's territory. The successive movements of the female in returning to her territory and her subsequent activities are indicated by the numbered open circles. Time at site 1, 10:02 A.M., juvenal, ● , left vicinity but female had not challenged it; 2, 10:07; 3, 10:11; 4, 10:20, ate something; 5, 10:24, at 10:27 tried unsuccessfully to catch small dipterans flying over water; 6, 11:00. Closed continuous lines represent rocks, dashed line the shoreline.

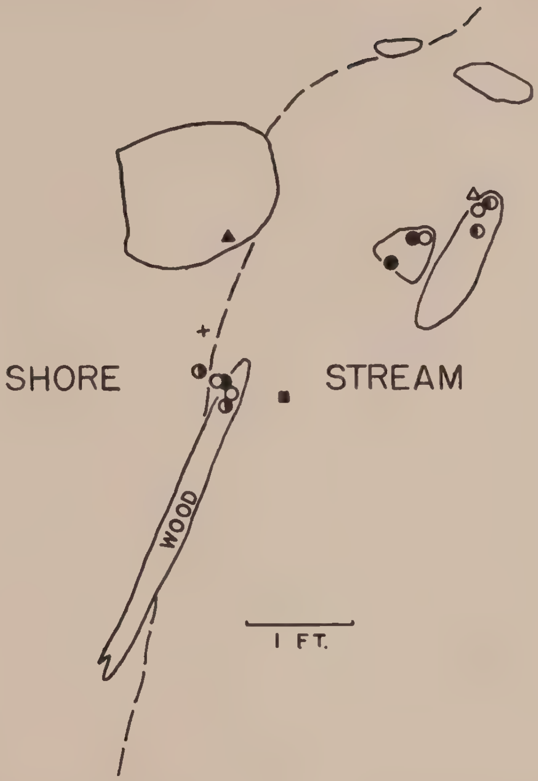


Fig. 5. The observed locations of a single *Prostherapis trinitatis,* female 8, over a period of 61 days. Extra-territorial journeys were made during periods of flooding and of artificial habitat change, but they are not indicated here. The symbols are as follows: July 1, ▬ ; July 5, ● ; July 8, ◐ ; July 10, ◑ ; July 14, ✚ ; July 24, ○ ; July 27, △ ; Aug. 10, Aug. 12, and Aug. 31, ▲ . Closed continuous lines designate rocks, dashed lines, the shoreline.

through the outermost set of points which represented places where the frogs were observed. The territories of the females were most often completely or partly surrounded by water. Ten of the 29 territories observed contained elevations, such as rocks, which were completely surrounded by water; 4 other territories were located on shore but with one edge of the territory bordered by water; the remaining 15 territories were centered about elevations, some of which were on shore while others were in the water.

The areas of the territories that were observed to be defended varied from 0.13 sq. ft to 2.43 sq. ft for 11 adult females, and the average area was 1.07 sq. ft. This represents the area occupied for a relatively short period, usually during an observation period of one hour. One large adult female, number 8, was readily identifiable from a distance because of a patch of yellow scar tissue on one heel. The movements of this animal were followed throughout the summer from July 1 until August 31 (Figure 5), and the area occupied during this period measured 48 in. by 24 in. by 36 in. and covered rocks in the water and logs and rocks on the shore. Three territories defended by subadult frogs were 0.40, 0.69, and 1.15 sq. ft in area, and the two defended by males were 0.36 and 1.21 sq. ft.

The density of the adult females remained relatively constant during the course of the study until the area was modified for experimental studies. Three counts of adult females present on the entire study area revealed that 7 were located on it on July 13, 9 on July 14, and 8 on July 27. All of the frogs were closely associated with water. Six other counts of adult females were made within a smaller part of the study area.

This part of the area supported the highest density of frogs, and the area consisted of 61% stream bed and 39% shore. The counts of the females located in this optimal area were: July 13, five; July 14, six; July 19, one; July 26, four; July 27, five; August 1, five. The average density was 4.3 females on this sub-unit of the study area. This relative constancy is probably maintained by the territorial behavior of the species, any excess adults being forced into other areas. Each adult female appeared to inhabit a discrete pile of rocks, more or less isolated from other rocks (Figure 6). This would reduce the number of interactions between females and tend to minimize density fluctuations.

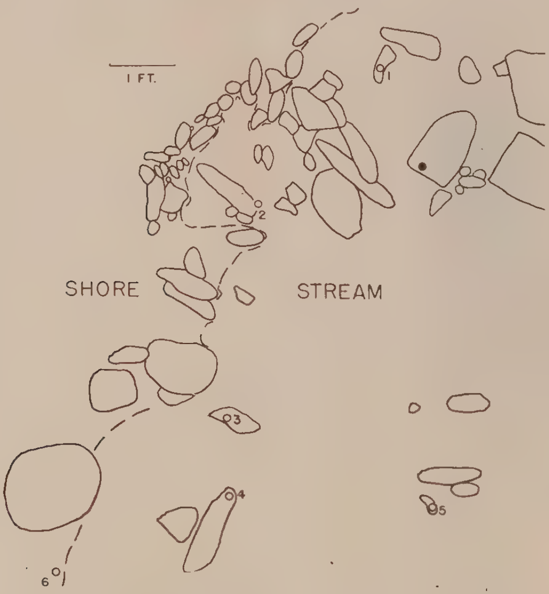


Fig. 6. The distribution of the adult females (numbered open circles) and adult male (solid circle) *Prostherapis trinitatis* in the census plot of the study area. The adults are usually found on elevated rocks in the stream or adjacent to it. Each frog tends to occupy a group of semi-isolated rocks. Closed continuous lines designate rocks, dashed lines, the shoreline.

Experimental Results

The experiments were carried out at one of the 3 study areas. Prior to the initiation of a test, the surface of the area in which the experiment was to be performed was usually cleared of all structures, such as sticks and stones, so that the surface was unobstructed. Certain man-made structures were then placed at various positions in such areas. These structures included piles of sand, and either single rocks or piles of rocks; these units were placed either on the shore or in the water. After the appropriate structures had been made, the area was left undisturbed for varying periods, usually about 5 days. During this period the frogs inhabiting adjacent areas moved into the experimental area. At the conclusion of this period the experimental structures were examined, and the number and kinds of frogs associated with the different structures were recorded.

It was apparent from field observations that *Prostherapis trinitatis* was most frequently associated with elevated structures. Since factors other than height of the structure above the surroundings could have been of importance in the occupancy of the area, a series of tests was designed to determine the nature of such possible factors. A plot 10 ft by 10 ft was divided into sixteen smaller quadrats, each quadrat measuring 2.5 ft on a side. The 16 quadrats were arranged in 4 rows and 4 columns. The 2 outer columns of quadrats were laid out on sandy beaches, one column on each side of a small mountain stream. The 2 inner columns included the stream, one column covering from midstream to one shore and the other column covering from midstream to the opposite shore. All naturally occurring elevations were removed from the plot. Eight of the qaudrats, 4 on shore and 4 in the water, remained without elevated structures, but various structures were placed in the remaining 8 quadrats. A single pile of sand, approximately 8-10 in. high was placed in each of 4 of the quadrats, 2 on land and 2 in the water. A flat rock having the same area as the sand piles was placed in each of the remaining 4 quadrats. On top of the rock were placed 2 small stones. Two of these quadrats were left as described, but sand was placed in all of the crevices of the remaining 2 structures (one of these structures was later washed away). The height and basal area of all of the structures were the same; they differed in the nature of the substrate, sand versus rock, and in the presence or absence of crevices.

The distribution of the frogs on the plot was noted one week later. Table I shows that 7 of the 8 frogs seen were associated with some elevation, and all 7 were on some elevation which had crevices. This experiment seems to indicate that elevation and crevices are both important in influencing the distribution of the frogs.

An additional experiment tested the importance of the crevices further. A study plot was set up on a sand bar completely surrounded by water. Nine points were arranged in 3 rows and 3 columns on this sand bar. The distance between neighboring points in any row or column was 3

TABLE I. The distribution of frogs relative to the position and type of experimental structure

Position	Kind of Structure	Number of Quadrats	Frogs
Shore	None	4	1 subadult
	Rocks with crevices	2	5 subadults
	Piles of sand	2	0
Stream	None	4	0
	Rocks with crevices	1	2 adult females
	Rocks without crevices	1	0
	Piles of sand	1	0

feet. An experimental structure was placed at each point. These structures were of 3 general types, (1) a pile of sand, (2) a single flat rock resting upon three small stones so that there was a single crevice beneath the rock, and (3) a pile of about 20 small stones heaped to form many crevices. The over-all basal dimensions of all structural types were 8 by 12 in.; there was one structure of each class in each column and row.

The study area remained undisturbed for a week before a census of the animals was made. No *P. trinitatis* were associated with type 1 structures; one adult female and 2 subadults were observed on or under type 2 structures; 3 adult females and 7 subadults were found on or under type 3 structures. These results corroborate the previous experiment and indicate that crevices are important in the selection of a territory.

Another experiment at the same location contrasted the suitability of an elevated rock with a single crevice beneath it (class A) and that of a similar rock with no crevice beneath it (class B). Each of the 3 structures, in each class, measured 8 by 10 by 12 in. The number of frogs on or under the structures was counted after a week had elapsed. Two adult females were observed on one of the rocks of Class A, but none was seen on any of the two other units of class A or of the three units of class B. However, 7 subadults were hiding in the crevices of the class A structures.

The next experiment attempted to determine the relationship between the area of the crevice and the number of frogs inhabiting it or the overlying rock. Five structures were placed on the periphery of a circular sandbar which was completely surrounded by water. At each location a flat rock was placed on top of 3 small stones so that a crevice was formed beneath the rock. Two other stones, each 4 x 5 in., were placed on top of each flat rock. The area of the flat rock differed at each site. The area of the rock at site 1 was 40 sq. in.; site 2, 77 sq. in.; site 3, 152 sq. in.; site 4, 162 sq. in.; site 5, 180 sq. in.

The area remained undisturbed for one week, and then the animals present on or under the structure were counted (Table II). It is evident that the number of animals found at each site tended to increase with the area of the crevice. The average area of crevice per frog varied from 40 to 81 sq. in. per frog.

TABLE II. The numbers of frogs associated with a single crevice of known area

Area of Crevice in sq. in.	Number of Frogs Present	Area of Crevice in sq. in./frog
40	1	40
77	1	77
152	3	51
162	2	81
180	4	45

A series of tests was conducted between August 8-26 to identify other structural features essential for areas which were occupied as territories by *P. trinitatis*. Each of the 10 experimental sites consisted of 3 flat rocks arranged so that each rock formed one side of a triangle. The flat upper surface of each rock projected above the water surface at a point about one yard offshore. These 10 sites were arranged into 2 groups, the first of 4 and the second of 6 units, and the 2 sets were separated by a rock dam. The 4 units of set one, numbered 1-4, were upstream from the dam and were placed at the corners of a square measuring 5 feet on a side. The shores paralleling these sites were covered with rocks and boulders. The 6 units of the second group, numbered 5-10, were downstream from the dam and were placed in 2 parallel rows 5 feet apart. There were 3 sites in each row, one every 5 feet. The shore nearest sites 5, 7, and 9 was sandy; that nearest sites 6, 8, and 10 was covered with rocks and gravel.

On certain days a 15 minute census was made of the numbers and classes of frogs present on the experimental structure. This census was taken 15 minutes after arriving on the area and after the activity of the frogs had returned to normal. During the 5 censuses made between August 9-13 fourteen animals were observed on the 10 units, 9 adult females, one adult male, and 4 subadults. Seven females and 3 subadults were seen at sites 1-4, those bordered shoreward and downstream by rocks. One female and one subadult were noted at sites 6, 8, and 10, those next to a rocky and gravelly shore. One male and one female were recorded at sites 5, 7, and 9, those paralleled by a sandy shore. These data indicate that the new sites closest to the pre-existing favorable areas were colonized first. They also show that the adult females are among the earliest colonizers.

On August 14, the shore along both sides of the stream was stripped of rocks and boulders for a distance of one yard from the water's edge. The dam was also removed, but the experimental units remained in place.

Censuses made between August 15-20 indicated a total of only 7 adult females on all 10 sites. The removal of the rocks along the adjacent shores reduced the habitat which served as a source of the frogs colonizing the new areas.

The distance of new areas from already existing sites was not the only factor affecting the colonization of these new areas, for it can be shown that the velocity of the water current between the sites and shore also influences colonization. The velocity of the water between the experimental structures and the shore varied from 1.5 to 2.0 ft per second. The position of some of the sites was shifted, altering the velocity of the current and the width of the water intervening between the sites and shore. Sites 1, 4, 8, and 9 were left in position as controls; sites 2, 5, and 10 were moved within 5-6 in. of shore, and the current velocity between the sites and shore varied between 0.6 to 1.0 ft per second; sites 3, 6, and 7 were placed with one apex on shore.

Twelve adult females, one adult male, and 2 subadults were observed on the structures between August 22-26. Only a single subadult was seen at any of the 4 control sites; 4 females and one subadult were noted on sites 2, 5, and 10, all just offshore; 8 females and one male were counted on the 3 structures abutting the shore. These results clearly indicate that proximity of suitable areas to shore is a factor in attracting frogs to these areas.

In connection with these experiments, it was frequently noticed that many frogs first occupied the sites as refuges. This series of tests was originally started August 7, but the structures were washed away that same day. They were replaced by 10:05 A.M. on August 8; by 10:20 A.M. a female had moved onto site 8; by 10:40 A.M. a second female took refuge from me by leaping from shore to site 7, but it returned to shore at 10:44 A.M.; at 10.42 A.M. a subadult and a female were observed at site 5, both having fled at my approach, and the female swam over to the dam at 10:46 A.M.; at 10:43 another female took refuge at site 10 but left almost immediately.

The final experiment was made to determine the upper surface area of the rocks most frequently occupied by *P. trinitatis*. Ten sites, 2 for each of 5 size classes, were located along the shore at the Iron Bridge Area. At each of the 10 locations a single rock was so placed that one end rested on the shore and the opposite projected into the water. The average areas of the rocks in the different classes were as follows: class 1, 312 sq. in.; class 2, 236 sq. in.; class 3, 131 sq. in.; class 4, 81 sq. in.; class 5, 55 sq. in. Two smaller stones, each approximately 24 sq. in., were placed on top of the basal rock at each site. These 2 stones produced extra crevices which could provide additional cover for the frogs, although they were constant for all 5 classes. The rocks were placed along parts of the shore covered with stones smaller than those used in the experimental units. Much of the surrounding area was covered with gravel or sand. Censuses were taken in the usual fashion between August 27-31.

There appears to be no absolute area of rock surface which is occupied preferentially by *P. trinitatis* within the range tested (Table III).

TABLE III. The total numbers of frogs associated with rocks of known surface area during five 15 minute census periods, Aug. 27-31

Class	Surface Area in sq. in.	Number of Frogs Present
1	312	2
2	236	5
3	131	4
4	81	6
5	55	3

The data suggest that rocks with a large surface area do not support as many frogs, in proportion to their size, as do the smaller rocks.

DISCUSSION

On the basis of the observational and experimental results it is possible to obtain some ideas about the physical structure of the *Prostherapis* territory. The total area defended is rather small, averaging 1.07 sq. in. for adult females, and such areas usually contain elevations which have crevices beneath them and which are alongside or surrounded by mountain streams. While it has not been shown that there is a definite relationship between the number of frogs occupying an elevation and the external surface area of that structure, there is a definite increase in the number of frogs as the number of crevices per elevation increases. The larger, presumably more aggressively successful, animals tend to occupy those sites containing all of the above features. The juveniles are more often distributed at greater distances from the water.

The elevations, streamside location, and crevices all appear to fulfill certain requirements in the natural history of these frogs. Feeding frogs usually sit on some elevation looking out over an expanse of open water. From such a position they can easily see any insects flying above the water and leap out at them. In addition, the residents are easily recognizable to potential intruders from these elevations, and, contrariwise, the residents can see any intruders trespassing upon the resident's territory. The streamside location serves several functions. Prey items, such as dipterans, are more abundant over the water than over the shore. The water frequently separates territories so that resident females are somewhat isolated from each other. This probably helps reduce aggressive encounters between adjacent frogs. Finally, the frogs take refuge in the water when they are disturbed. The crevices also appear to function in this manner, the frogs taking refuge in them upon disturbance. Of more importance is the fact that the presence of crevices makes it possible for more than one frog to inhabit a rather restricted area. For example, the data from Table II indicate that more than one individual can be found in a single crevice. Prior to the census reported in Table II, observations were made on the number of frogs observed to be active at the surface of the structures. Single individuals were observed on 3 of the structures. All other frogs associated with the 5 structures were in the crevices. These crevices would function in 2 ways: first, by enabling the smaller frogs to escape the aggressive actions of the larger ones; secondly, by inhibiting normal territorial responses elicited in the open.

SUMMARY

1. Observational and experimental studies were made of the behavior and territory of the dendrobatid frog, *Prostherapis trinitatis,* inhabiting the mountain streams of the coastal mountains of north central Venezuela.

2. The females are larger and more prominently marked than either the adult males or the subadult animals. Adult females, adult males, and subadults all defend small areas, terrritories, against invasion by other members of the same species. The females do so more commonly than the other 2 classes.

3. The adult females tend to be found nearer the stream than do the subadults. The adult males are not as sedentary as the other 2 classes.

4. Individuals of all classes left the territory when disturbed by moving animals or flooding.

5. The average area of the territory of the adult females was 1.07 sq. ft.

6. The density of the females remained relatively constant. It could not definitely be determined if the territorial behavior of the frogs was responsible for the even spacing of the frogs.

7. Territories of adult females are centered about elevations, particularly rocks, which are surrounded or bordered by water. The territories tend to be centered around discrete groups of rocks.

8. Elevations with crevices in them were occupied more readily than elevations without crevices.

9. The numbers of frogs inhabiting an elevated structure increased as the number of crevices increased.

10. Proximity to occupied areas and distance from shore were other factors affecting the occupancy of midstream areas.

11. The exposed surface of the occupied rocks does not appear to be a very important factor in determining distribution of the frogs.

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THE INTERRELATIONSHIPS OF LOGGING, BIRDS, AND TIMBER REGENERATION IN THE DOUGLAS-FIR REGION OF NORTHWESTERN CALIFORNIA

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Intensive logging of a virgin stand of Douglas-fir (*Pseudotsuga menziesii*) began in 1950 in the inner coast ranges of northwestern California. Most timber is being clear cut in blocks of from 10 to 20 acres. Intervening blocks of roughly equal size are left for a later cutting and meanwhile serve as seed sources for the cutovers. Initial efforts to seed coniferous trees on these blocks by artificial or natural means have been discouraging. Rodents and other seed-eating animals flourish after logging, and play a major role in retarding or preventing regeneration.

The subject of animals as destroyers of conifer seed has been discussed by Smith and Aldous (1947), who reviewed the literature and listed all birds and mammals known to eat coniferous seed in the United States. Rodents, particularly mice of the genus *Peromyscus,* have long been recognized as the chief consumers. Studies of the local distribution and food of two species of *Peromyscus* on timberland in California have been made by Jameson (1951 and 1952). The responses of small mammal populations to logging of Douglas-fir were studied by Tevis (1956).

Further information on animal factors that hinder reforestation is needed by the forester and an understanding of how logging alters the fauna is of value to the ecologist and land manager. Toward these ends, this study of forest birds was made in cooperation with the California Forest and Range Experiment Station on the Six Rivers National Forest near Salyer in Trinity and Humboldt Counties, California. The purpose of the investigation was to determine changes in species composition, numbers, food habits, and activities of bird populations immediately after the forest is logged and during the first few years after logging when regeneration of timber is most endangered by biological and physical adversity. The effect of environmental changes on populations of forest birds have been studied by Lack (1933, 1939, and 1951) in English pine plantations, and by Odum (1950) in successional stages toward climax hardwood and hemlock forest of the Highlands Plateau in North Carolina. Studies by Turcek (1952 and 1956) were concerned with bird populations of spruce and other forest types in Czechoslovakia.

STUDY AREAS

Twenty cutover and virgin forest areas were censused regularly for a period of 3 years. These consisted of 7 weed-stage cutovers 1-2 years old, 8 brush-stage cutovers 3-7 years old, and 5 virgin forest areas. Census time for the 3 vegetative types was 274, 460, and 260 hours, respectively. Young cutovers were distinguished from older brushy cutovers by the marked abundance of Australian fireweed (*Erechtites arguta*) and a relative scarcity of weeds and shrubs that invade 2 years after an area is logged. Thus, data on relative abundance of birds are presented for 2 types of cutovers as well as for the virgin forest.

Plant densities were obtained for some representative areas (Table I). The number of plants per acre was estimated on cutovers that were 2, 3, and 5 years old and on 2 virgin forest tracts by counting all plants in circular sample plots with a 25-foot radius. Ten such samples were taken in each area. The Friday Ridge Forest (D in Table I) is most typical of the region at elevations below 4,000 feet. It consists of a nearly homogeneous stand of mature and over-mature Douglas-fir with a dense brushy understory of tan oak. At elevations above 4,000 feet, other conifers are mixed with the fir and there is a greater variety of understory species. Happy Camp Mountain Forest is an example.

The percentage of ground covered of herbaceous plants, low brush, and other materials was estimated from sample plots on 3 of the areas to determine changes that occur in ground cover after logging (Table II). I rely on a census made by the Experiment Station for the data on the Brush Mountain cutover when it was 2 years old; mil-acre plots were used instead of 25-foot circles, but for purposes of this study, results from the 2 sampling methods are comparable.

The most important plant producing animal food in the region are Douglas-fir, tan oak, and Pacific madrone. Crops of these major tree species differed considerably in each year of the study. In 1955, the Douglas-fir seed crop was poor except in a few locations, but both tan oak and madrone bore heavily. In 1956, Douglas-fir produced its first good crop in 6 or 7 years. This crop might not have been utilized so heavily by wildlife if tan oak and madrone had not had a

TABLE I. Number of plants per acre on representative cutovers and virgin forest areas of the inner north coast range, California

	CUTOVERS			FOREST	
	A	B	C	D	E
	Zeigler Point Cutting Block "A"	Zeigler Point Cutting Block "B"	Brush Mtn. Cutting Block "A"	Friday Ridge Virgin Forest	Happy Camp Mtn. Virgin Forest
Years after logging	2	3	5	—	—
Sugar pine, *Pinus lambertiana*	—	—	—	—	2
Ponderosa pine, *Pinus ponderosa*	1	—	11	—	2
Douglas-fir, *Pseudotsuga menziesii*	—	—	244	111	153
White fir, *Abies concolor*	—	—	—	—	666
Incense cedar, *Libocedrus decurrens*	—	—	—	—	64
Western yew, *Taxus brevifolia*	—	—	—	—	9
Hazel, *Corylus rostrata*	—	1	29	7	49
Canon oak, *Quercus chrysolepis*	2	1	—	—	22
California black oak, *Quercus kelloggii*	2	—	—		
Tan oak, *Lithocarpus densiflora*	10	35	743	1717	222
Giant chinquapin, *Castanopsis chrysophylla*	—	—	—	4	15
Currant, *Ribes nevadense*	—	—	2	—	—
Gooseberry, *Ribes roezlii*	1	23	66	—	18
Thimble berry, *Rubus parviflorus*	—	—	91	—	—
Western raspberry, *Rubus leucodermis*	—	10	207	—	
California blackberry, *Rubus vitfolius*	—	1	51	—	
Wood rose, *Rosa gymnocarpa*	—	1	51	100	240
Poison oak, *Rhus diversiloba*	—	—	20	4	—
Big-leaf maple, *Acer macrophullum*	—	—	36	2	—
Tobacco brush, *Ceanothus velutinus*	—	—	195	—	—
Deer brush, *Ceanothus integerrimus*	—	1	87	—	—
Blackfruit dogwood, *Cornus sessilis*	—	—	2	7	—
Mountian dogwood, *Cornus nuttallii*	—	—	11	—	9
Madrone, *Arbutus menziesii*	1	1	36	2	337
Green manzanita, *Arctostaphylos patula*	—	1	11	—	
California huckleberry, *Vaccinium ovatum*	—	—	9	—	
Blue elderberry, *Sambucus glauca*	—	—	22	—	
Coyote brush, *Baccharis pilularis*	—	5	—	—	—

relatively light crop that year. In 1957, both Douglas-fir and madrone corps failed and the tan oak acorn crop was relatively light. When any one of the 3 chief food-producing trees had a heavy crop, that food was available and used by wildlife from September through March or even into May. When none of these major foods was available, birds that usually ate them turned to insects, berries, weed seeds, and grass seeds.

METHODS AND RESULTS

There are 2 main approaches in determining or analysing bird abundance. A measurement of actual population expressed in terms of area of known size is most desirable. However, it is easier to measure relative numbers. In this study, relative abundance trends were followed in each of the 3 habitat types over the 3-year period. Estimates of actual numbers were made on 2 areas during the spring of each year.

TABLE II. Percentage ground cover of cutovers and virgin forests of the inner north coast ranges, California

	CUTOVERS		VIRGIN FOREST	
Kind of cover	C 2 years old[1]	C 5 years old [1],[2]	D Douglas fir[2]	E Mixed conifer[2]
FERNS				
Pteris aquilina	2	2	—	—
Polystichum munitum	—	—	1	4
GRASSES, RUSHES, SEDGES	1	2	—	—
HERBS				
Erechtites arguta, Australian fireweed	17	—	—	—
Cirsium lanceolatus, Bull thistle	—	2	—	—
Whipplea modesta, Whipplea	9	16	4	7
Lathyrus torreyi, Pea	—	4	—	—
Montia spp., Miners lettuce	1	1	—	—
Epilobium paniculatum, Willow herb	1	1	—	—
Berberis spp., Oregon grape	—	—	2	4
Achlys triphylla, Deer-foot	—	—	3	7
Chimaphila umbellata, Prince's pine	—	—	5	9
Other	4	4	2	4
BRUSH				
Lithocarpus densiflora, Tanoak	9	16	18	5
Rubus leucodermis, Western raspberry	—	2	—	—
Ribes roezlii, Gooseberry	—	2	—	—
Rhus diversiloba, Poison oak	—	1	—	—
Ceanothus velutinus, Tobacco brush	1	5	—	—
Arbutus menziesii, Madrone	—	—	—	3
Other	1	3	2	2
Slash	29	18	12	10
Duff	6	7	50	40
Bare soil, rocks	19	14	1	5
Total	100	100	100	100

[1] Based on 560 milacre plots.
[2] Based on circular plots of 25 foot radius.

Censuses to obtain relative abundance were made 8 or 10 times a month in each of the vegetative types. Each census was usually over an hour in duration. During this time, the observer walked slowly about or stood at places where the entire area could be watched. All species and numbers of birds seen or heard were recorded (Table III), as was their activity and the type of vegetation which they frequented.

Indices of abundance were derived by combining the average number of individuals seen per census with the percentage of all censuses that the species was observed. The method is described fully by Kendeigh (1944). In the present study, comparison of these indices with actual abundance figures showed that they were roughly equal to the number of birds per 20 to 30 acres, the size of a single large cutover. Average relative abundance of the common birds of cutovers and Douglas-fir forest for the entire 31-month study period is shown (Figure 1).

During the breeding seasons, actual population size was estimated by delimiting territories of pairs of birds on one 13-acre brush-stage cutover and one forest area of similar size; the vegetation of these areas is listed (C and E in Tables I and II). Early morning counts were made

TABLE III. Birds of cutover and virgin Douglas-fir forest. Figures are indices of abundance. P: present, C: common, R: resident, Sp: spring, Su: summer, F: fall, W: winter

Species	Coniferous forest	Weed cutover	Brush cutover	Season
California quail, *Lophortyx californica*	—	P	P	R
Mountain quail, *Oreortyx picta*	—	.8	3.2	R
Band-tailed pigeon, *Columba fasciata*	.7	—	.9	FW
Turkey vulture, *Cathartes aura*	—	P	P	SpSuF
Sharp-shinned hawk, *Accipiter striatus*	.6	.4	.6	R
Red-tailed hawk, *Buteo jamaicensis*	—	.6	1.3	R
Spotted owl, *Strix occidentalis*	P	—	—	R
Screech owl, *Otus asio*	P	P	P	R
Horned owl, *Bubo virginianus*	P	P	P	R
Pigmy owl, *Glaucidium gnoma*	P	—	—	R
Hairy woodpecker, *Dendrocopus villosus*	.8	3.0	3.0	R
Downy woodpecker, *Dendrocopus pubescens*	.4	.4	.7	R
White-headed woodpecker, *Dendrocopus albolarvatus*	P	—	P	R*
Red-breasted sapsucker, *Sphyrapicus varius*	.9	1.0	1.3	R
Pileated woodpecker, *Ceophloeus pileatus*	1.7	—	—	R
California woodpecker, *Balanosphyra formicivora*	—	3.7	12.6	R
Red-shafted flicker, *Colaptes cafer*	1.8	2.2	3.7	R
Allen's hummingbird, *Selasphorus sasin*	—	—	P	Su
Olive-sided flycatcher, *Nuttallornis borealis*	—	—	C	Su
Hammond flycatcher, *Empidonax hammondi*	C	—	—	Su
Wood pewee, *Contopus richardsoni*	C	—	C	Su
Steller jay, *Cyanocitta stelleri*	9.9	7.6	14.7	R
Oregon jay, *Perisoreus obscurus*	P	—	—	R*
Raven, *Corvus corax*	C	—	P	R
Evening grosbeak, *Hesperiphona vespertina*	.5	—	.2	R
California pruple finch, *Carpodacus purpureus*	.5	.9	.9	R
Red crossbill, *Loxia curvirostra*	.8	3.1	2.2	R
Green-backed goldfinch, *Spinus psaltria*	—	.9	2.4	SpSuF
Pine siskin, *Spinus pinus*	2.1	4.3	4.8	R
White-crowned sparrow, *Zonotrichia leucophrys*	—	.2	.3	SpF
Golden-crowned sparrow, *Zonotrichia coronata*	—	.9	2.4	SpF
Oregon junco, *Junco oreganus*	9.7	14.6	22.9	R
Fox sparrow, *Passerella iliaca*	—	.4	1.4	FW
Spotted towhee, *Pipilo maculatus*	—	.6	2.6	R
Black-headed grosbeak, *Pheucticus melanocephalus*	.3	.1	2.1	SpSu
Lazuli bunting, *Passerina amoena*	—	P	C	SpSu
Western tanager, *Piranga ludoviciana*	.2	.7	1.7	SpSu
Cassin vireo, *Vireo solitarius*	C	C	—	SpSu
Calaveras warbler, *Vermivora ruficapilla*	—	—	C	SpSu
Hermit warbler, *Dendroica occidentalis*	C	—	—	SpSu
Tolmie warbler, *Oporornis tolmiei*	—	—	C	SpSu
House wren, *Troglodytes aedon*	—	P	P	SpSu
Winter wren, *Troglodytes troglodytes*	1.7	6.5	6.1	FWSp
Creeper, *Certhia familiaris*	C	—	—	R
White-breasted nuthatch, *Sitta carolinensis*	—	P	P	SpF
Red-breasted nuthatch, *Sitta canadensis*	12.2	—	—	R
Mountain chickadee, *Parus gambeli*	P	P	P	R*
Chestnut-backed chickadee, *Parus rufescens*	11.0	4.4	3.6	R
Bush-tit, *Psaltriparus minimus*	—	—	P	R
Golden-crowned kinglet, *Regulus satrapa*	6.6	4.0	1.4	FWSp
Ruby-crowned kinglet, *Regulus calendula*	—	—	P	SpF
Hermit thrush, *Hylocichla guttata*	1.7	.4	.6	R
Townsend's solitaire, *Myadestes townsendi*	P	P	—	R*
Varied thrush, *Ixoreus naevius*	4.4	7.5	8.0	FWSp
Western bluebird, *Sialia mexicana*	—	P	P	W

* At high elevations only.

every one or 2 weeks from late April until early July; 7 were made on each area every year. During each visit, the locations of all birds seen and heard were marked on grid maps of the areas. Territories were mapped at the end of each season and the number of pairs per 100 acres was calculated for each type (Table IV).

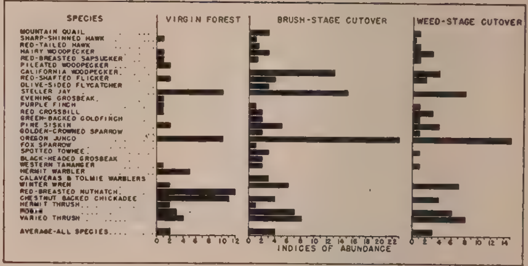

FIG. 1. Comparative abundance of the common birds of cutover and virgin forest areas, 1955-57.

TABLE IV. Numbers of bird territories on cutover vs. virgin Douglas-fir forest during the breeding season (Numbers in parentheses are pairs/100 acres)

	BRUSH MTN. CUTTING BLOCK "A" (13 acres)			HAPPY CAMP MTN. VIRGIN FOREST (25 acres)	
Year	1955	1956	1957	1956	1957
Years after logging	3	4	5	—	—
Number of censuses	7	8	7	7	7
Mountain quail	2 (15)	2 (15)	1 (8)	—	—
Pigmy owl	—	—	—	¼ (1)	—
Hairy woodpecker	¼ (2)	1 (8)	1 (8)	¼ (1)	1 (4)
Red-breasted sapsucker	—	—	—	1½ (5)	1 (4)
Pileated woodpecker	—	—	—	¾ (3)	¾ (3)
California woodpecker	2½ (20)	2 (15)	2 (15)	—	—
Red-shafted flicker	1½ (12)	1 (8)	1 (8)	¼ (1)	—
Western flycatcher	—	—	—	3 (12)	1½ (6)
Olive-sided flycatcher	—	1 (8)	1 (8)	—	—
Steller jay	1½ (12)	1 (8)	1 (8)	¾ (3)	3 (12)
Oregon junco	5½ (42)	7 (54)	6 (46)	5 (19)	4 (17)
Spotted towhee	—	1 (8)	1 (8)	—	—
Black-headed grosbeak	½ (4)	½ (4)	—	—	1 (4)
Hermit warbler	—	—	—	12½ (48)	8 (32)
Winter wren	—	—	—	—	¼ (1)
Creeper	—	—	—	—	1 (4)
Red-breasted nuthatch	—	—	—	3 (12)	2½ (10)
Chestnut-backed chickadee	2¼ (18)	1½ (12)	2 (15)	2 (8)	3 (12)
Goiden-crowned kinglet	—	—	—	—	1 (4)
Hermit thrush	—	—	—	2 (8)	1 (4)
Robin	½ (4)	—	—	—	—
Totals	16.5 (125)	18.0 (140)	16.0 (128)	31.3 (121)	29.0 (117)

An attempt was made to check actual population size in fall by means of trapping and coloring birds with food dye. If successful, ratios of colored birds to number of birds observed in subsequent checks could be used to determine population size. The test was unsuccessful because of the rapid turnover of individuals on the study area at that time of year.

With juncos, the need for elaborate census work was questioned when relatively compact flocks could be so easily counted as the individuals followed each other from one foraging spot to an-

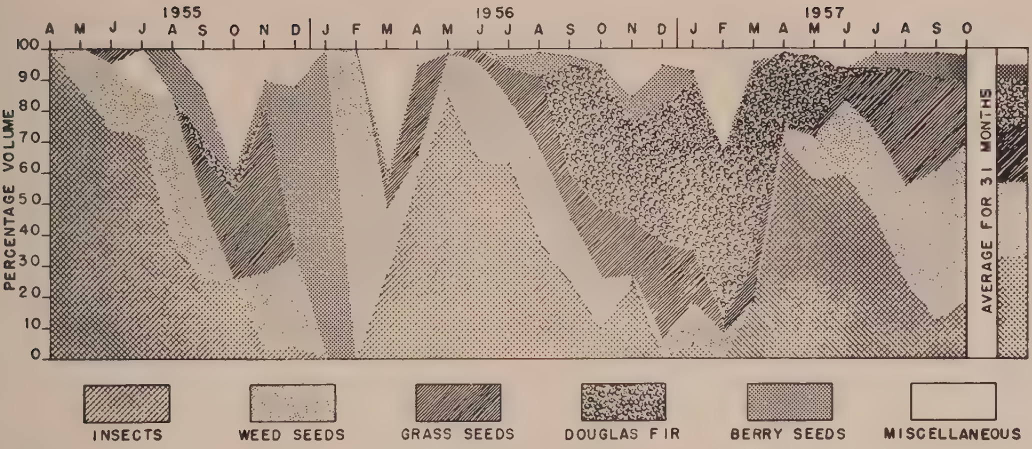

Fig. 2. Monthly food consumption by juncos, April, 1955 through October, 1957.

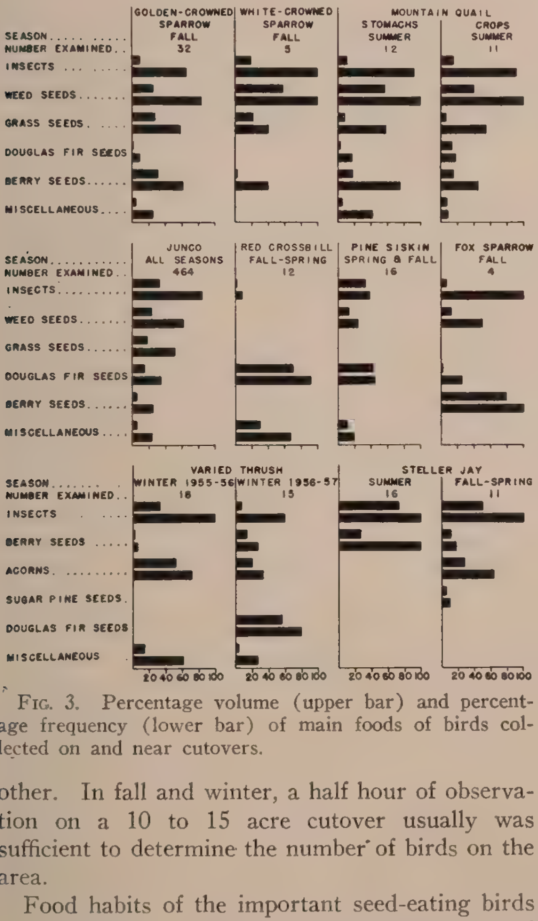

Fig. 3. Percentage volume (upper bar) and percentage frequency (lower bar) of main foods of birds collected on and near cutovers.

other. In fall and winter, a half hour of observation on a 10 to 15 acre cutover usually was sufficient to determine the number of birds on the area.

Food habits of the important seed-eating birds of cutovers were studied by field observation and examination of stomach contents. Food habits of juncos were studied in detail; percentage volume and percentage frequency of occurrence of the chief kinds of food in their stomachs were computed by monthly intervals. In addition, nearly all of the plant seeds found in the stomachs were identified to species, or at least to genus. Percentage volume of the most important of these seeds was calculated. Figure 2 shows the proportions in which the various food items occurred during the 31-month period. Nine other species of birds were collected when they were abundant and their stomach contents analyzed (Figure 3).

Juncos and most of the other birds studied have no crops. Gullet contents were found in only 12% of juncos examined, so most of the data on their diet had to be based solely on gizzard contents. Proportions of food items are represented less accurately here than in gullet, for softer foods may be so finely crushed as to be undetected while more resistant seed coats, berry seeds, and the hard parts of insects are likely to be overemphasized.

In stomach examinations, the proventricular and gizzard contents were spread out with water in a petri dish under a dissecting microscope and percentage volume of each kind of food was estimated. The final estimate usually was derived from a series of sample estimates from small areas of the dish covered by the field of the scope.

ACCOUNT OF SPECIES

Oregon junco

The most numerous of all birds that occupy cutover forest land in the Douglas-fir region is the junco. It is versatile in its choice of habitat and is the only ground feeder present in numbers every month of the year. Its fondness for seed of Douglas-fir was demonstrated during times when the seeds were available.

The number of juncos occupying a freshly logged area is approximately equal to that in the

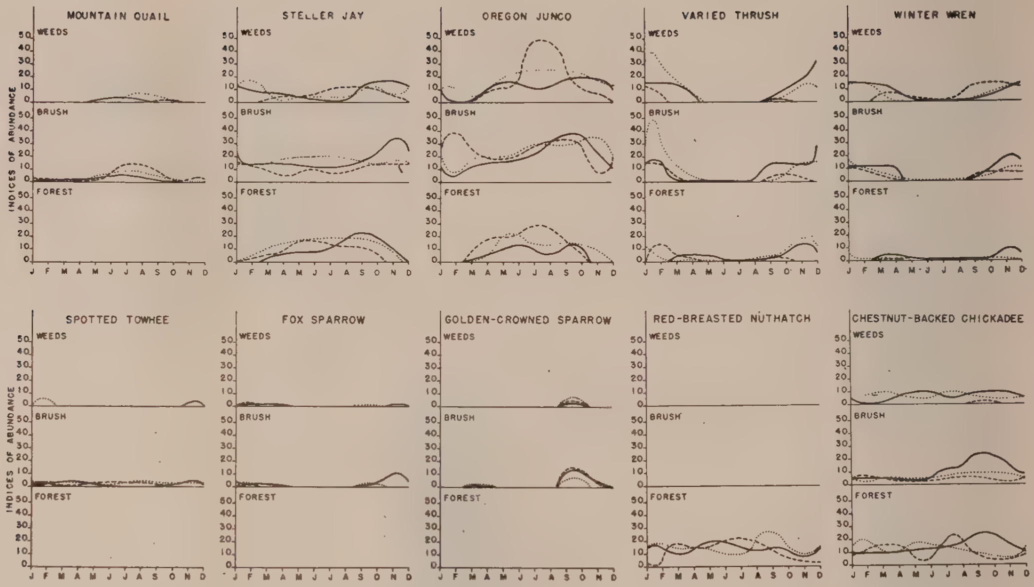

FIG. 4. Relative abundance of the common birds of cutover and virgin forest areas 1955-57. Solid lines; 1955, dotted lines: 1956, broken lines: 1957.

uncut forest. As weedy vegetation (predominantly Australian fireweed) develops, the population increases; it reaches its peak 3 to 6 years after logging when brush is becoming the dominant form of vegetation (Fig. 1). At this time the population density may be 2 or 3 times that in the virgin forest. There was an indication of slight decline on the oldest areas censused.

Figure 4 shows relative abundance trends of juncos and 9 other important species in 3 habitat types. Lowest numbers usually occurred in January and February. Residents were supplemented by migrants in March and April. High populations came in August and September after the breeding season and at the beginning of fall migration. Numbers remained high through October and, in years when little or no Douglas-fir seed was produced, decreased markedly in late November and December. The exception to the rule of decreasing numbers in winter occurred at the time of Douglas-fir seed abundance in the winter of 1956-57. Junco numbers remained very high on brush-stage cutovers that winter.

The foods of juncos were determined by field observation and by examination of 460 stomachs. Most of the stomachs were from birds that had been feeding on cutovers, though about 50 birds were collected in the forest.

Insects, particularly small beetles, were a substantial part of the spring diet each year. Seeds of miner's lettuce (*Montia perfoliata* and *M. diffusa*), common early-seeding plants of cutovers, complemented the spring insect diet. These seeds became most utilized in June of each of the 3 years, at which time they constituted from 21 to 32% of the food volume. In summer, juncos depended heavily on the seeds of a great variety of weeds and grasses, the most important of which were bull thistle, western fescue, bluegrass, hairgrass, knotweed, Australian fireweed, and panicled willow herb. Fruits of western raspberry and, in the forest, strawberry (*Fragaria californica*) were of some importance in late summer.

Fall and winter diet varied considerably from year to year, depending upon the availability of different foods. In 1955-56, fruit of Pacific madrone was used extensively during the winter, along with herb and grass seeds. Douglas-fir seeds were a minor food at scattered locations in the fall of 1955. Birds were relatively scarce on cutovers during the winter.

Douglas-fir produced an abundant supply of cones during the summer of 1956. The seeds first appeared in junco stomachs on September 15 and constituted more than 50% of the food volume during that fall and winter. As many as 40 seeds were found in the gullet of a single junco. Birds were more abundant in logged areas during the winter of 1956 than in the preceding or succeeding winters.

Douglas-fir seed continued to be an important food of juncos through the spring of 1957. Germinating seeds and very young seedlings were found in stomachs at this time. Insects were less important than they had been the previous 2 years, though they still made up 60% of the volume. Consumption of fir seeds decreased by June and, with no new seeds produced, this food source was entirely eliminated by September. The birds then turned to seeds of grass and weeds. Very few juncos were present on any of the cutovers by November, possibly because of food scarcity.

The junco almost invariably forages on the ground but on one occasion in winter a large flock was seen swarming finch-like after seeds in the cone-laden crowns of a group of Douglas-firs. Usually, when seeking fir seed, they foraged in skid roads and other open spots on the ground. The birds obviously influence forest regeneration when they feed along the edges of cutovers on good potential seed beds where seed fall is heaviest.

The large amounts of logs and other slash left by most logging operations provide good resting and escape cover for flocks of resident juncos. The birds are particularly dependent on this cover on areas before the invasion of brush. Thus, removal of logging debris constitutes a good control measure for juncos.

Cutovers, especially those in the brush stage, make good breeding grounds for juncos. Male birds begin to sing from their tree-top perches in late February. Winter flocks break up during March and pairing is noticeable by late April. During May, pairs occur on brush-stage cutover blocks at a density of about one pair to 2 acres. Nest building is in process by late May. The birds invariably use dense clumps of *Whipplea modesta* for nest sites. Fledged young may be seen before the last week in June and a second nesting often occurs in July. All of the season's young are flying by late July.

On the 13-acre brush-stage cutover (Table IV), 5 to 7 pairs of juncos usually were successful in raising 3 or 4 young apiece. The birds congregated in early August in flocks which ranged from 32 to 50 in size. At the time of the first of the fall rains, usually in late September, the resident flocks were augmented by migrants. Except in the year of fir seed abundance, junco populations on cutovers decreased sharply in November.

Some tests with marked birds indicated that fall is a time of wandering and mixing of flocks. Two 15-acre cutover blocks separated by a timbered spur ridge each held a flock of about 30 to 40 birds during the fall of 1957. A live trap was kept operating on both areas and every 2 weeks parts of each flock were captured and marked with diagnostic colors (food dye). Birds from each flock readily mingled with those of the other flock. Some individuals left the area entirely. At least 2 birds wandered as far as 2 and 3 miles from the trapping sites. While wandering and mixing of flocks occurred freely during October and the first part of November, the actual flock size on each cutover changed little. Individuals did not become committed to one flock or one foraging area until December. Except in periods of snowy weather, flock size and flock membership remained relatively stable from December through March.

To sum up, logging of the forest provides optimum conditions for population increase in juncos which thus becomes the most important of the birds hindering reforestation by feeding on naturally falling Douglas-fir seed.

Varied thrush

Varied thrushes are among the most common birds in the region in winter, but are scarce from late April until mid-September. They are found at the edges and brush thickets of cutovers more frequently and in greater numbers than in the coniferous forest. Concentrations are particularly heavy in stands of tan oak. Their response to fluctuating weather conditions was more marked than that of other species. During mild weather with retreating snow cover, they disperse widely through the mountains so that only small inconspicuous groups can be found in the damp, dark recesses of the virgin forest. Snow and cold immediately force them to concentrate in large numbers at low elevations. A few birds may be found in heavily forested canyons in summer.

Thrushes were most abundant in the winter of 1955-1956 when there was a large crop of madrone berries. They were least abundant in the fall of 1957 when all 3 of the important food-producing trees failed to produce good crops. On the basis of field observation, tan oak acorns and madrone berries appeared to be the chief foods during 3 of the 4 winters of the study. Acorns were obtained on the ground; madrone berries were gleaned from the crowns of the trees. Douglas-fir seed was an important food during the winter of 1956-57. Stomach contents of 33 varied thrushes were examined (Fig. 3).

The thrush may be ranked as probably second to the junco in importance as a ground consumer of fir seed. It exerts a beneficial effect through its consumption of seed of tan oak and madrone, both of which offer serious competition to Douglas-fir. The bird also eats many insects.

Spotted towhee

Before logging operations were started in the region, towhees where restricted to manzanita and ceanothus brushfields on poor timber sites; now they occupy brushy cutovers as well. In some instances, as in winter when snow forces the birds to concentrate at low elevations, they are found on the recent weedy cutovers, but usually they do not appear until 4 years after logging. On old brushy cutovers, they are permanent yearlong residents at a density of one or 2 pairs per 15-acre cutover block. There was little evidence of migration or shifting except during snowy periods. Spotted towhees nested and raised young on brush-stage cutovers from 4 to at least 7 years after logging. A population increase may be expected as more acreage reverts to brush. The bird is not a serious threat to Douglas-fir regeneration as it occupies sites that have already produced or lost the opportunity to produce young trees from natural seedfall.

Mountain quail

Logged areas are used extensively by quail during the nesting season and through the summer. Although cutovers are preferred, it was common to see the birds on newly logged areas. Three or 4 broods were sometimes seen on one cutover at the same time. Every brushy cutover had two or more pairs during the breeding season. The decrease in numbers in fall and winter (Fig. 4) is probably more apparent than real because quail presence was frequently determined on sound evidence alone and the birds are relatively silent at that time of the year.

Some of the more important foods found in crops and stomachs of 12 birds shot in late summer are given in Fig. 3. Seeds of Australian fireweed, bull thistle and tarweed (*Madia* spp.) were chief among weed seeds. Black raspberries and seed of poison oak were also important.

Logging, then, is a stimulus to population growth in mountain quail. This species took some fir seed in the fall of 1956 but has a minor deterrent effect on timber regeneration.

Sparrows

In the fall, both fireweed and brushy cutovers attract large numbers of migrating golden-crowned sparrows. They invade the areas in late September and become an important part of the ground-feeding bird population during September and October; most are gone by late November. White-crowned sparrows are often present in lesser numbers at the same time. A few birds of both species visit again on their way north in spring. Crowned sparrows ate some Douglas-fir seed during the fall of 1956 but seed of fescue grass, Australian fireweed, and bull thistle were the chief food every fall.

Fox sparrows are common on brushy cutovers and occasional on fireweed cutovers from October through April but were not observed in forested areas. They sometimes forage in sizable flocks, especially in late fall when as many as 20 may be seen on a single cutover. This species breeds at the highest elevations in the region. No birds were found on logged areas during the breeding season, probably because none of the cutovers was high enough.

Fox sparrows were seen taking Douglas-fir seed that had fallen on a cutover so they are probably detrimental to forest regeneration. They ate berries of madrone, but seeds and berries of the cutover shrubs, such as elderberry, gooseberry, huckleberry, salal (*Gaultheria shallon*), and some forms of ceanothus, were the most important foods.

Steller jay

Opening of the forest by logging results in an increase in the jay population, though the increase in numbers above those in the forest does not occur immediately. The birds seldom used cleared areas until after these had passed through the weed stage, although the large firs and the scattered tan oak and madrone trees that are left standing in cutovers are important for the jay. Here they pursue insects that inhabit the trunks and foliage; less often they hunt insects among the logs and slash. The birds reach their greatest numbers on brush-stage cutovers in late summer and early fall when they flock onto these areas for various berries. In winter they forage extensively in tan oak in cutovers. The birds prefer cutovers to the forest in winter (Fig. 4).

Observations and analyses of stomach contents indicate that insects and acorns are preferred foods of the jay. No Douglas-fir seed was found in the stomachs examined and no birds were seen eating it. In late summer and early fall they feed on black raspberries, blackberries, currants, and elderberries. Sugar pine seed was much in demand in the few places where it was available in the fall of 1956. The birds gathered this seed by shaking it loose from the cones on the trees.

Winter wren

The winter wren was equally abundant on weed and brush cutovers where it was invariably seen in close association with logs. On some cutovers, culled logs form 25% of the ground cover and, on such areas, wren populations rapidly become two or three times as large as on other cutovers. I have seen wrens concentrating on areas where yarding of logs was still in process, and flitting about decks of logs even as they were being loaded onto the trucks. Present efforts to clear all slash from logged areas will bring about a marked reduction in numbers of wrens.

Winter wrens leave the cutovers in April and do not return until October. Some breed in heavily forested canyons and at the highest elevations about Salyer, but they are mostly absent from the Douglas-fir belt in summer. The house wren takes their place at this season and occasionally nests on cutovers.

No change in numbers or habits of this species was noted during the year of heavy Douglas-fir seed production. They did not seem to be important as seed consumers on any of the study areas but no stomachs were examined. Moore (1940) lists the winter wren as a consumer of Douglas-fir seed.

Tree-foraging seed-eating birds

Several species of birds that were seldom seen on cutovers were common in the surrounding forest. These influenced conifer regeneration on cutovers when they fed on Douglas-fir seed from cones in trees bordering logged areas.

Chestnut-backed chickadees and red-breasted nuthatches were the most abundant of this group of birds. Pine siskins and green-backed goldfinches came to cutovers in summer to raid thistle and Australian fireweed seed, but usually confined their activities to the forest. Purple finches and evening grosbeaks were regular residents in the forest canopy, at least in winter. Red crossbills were numerous during the period of fir seed abundance in late 1956 and early 1957. All of these species were seen taking seeds from cones in the crowns of firs near cutovers and are a factor in reducing seed abundance before it even reaches the ground. Sometimes flocks of these birds feeding in the crowns of coneladen firs will loosen more seeds than they eat. The resulting shower of seeds is then spectacular and attracts ground-feeding chipmunks and juncos.

Woodpeckers

Woodpeckers seem to increase in numbers after logging. Apparently logging slash and isolated standing trees, many of them dead or dying, make logged lands as suitable as the virgin forest for flickers and hairy woodpeckers. An increase in tan oak acorn production that is stimulated 3 years after logging is accompanied by increasing numbers of California woodpeckers. In the fall they stud all available snags with acorns and live on the store through the winter. Where the pure Douglas-fir forest gives way to mixed conifers at an elevation of 4,000 feet, the California woodpecker is replaced by the white-headed woodpecker. The latter is quite destructive to pine cones (Tevis 1953). Pileated woodpeckers had no important effect on the Douglas-fir seed crop in 1956. Flickers have been recorded as consumers of coniferous seed (Taylor and Gorsuch 1932).

Summer birds

Some insectivorous birds occupied the census areas in summer only. The most common were the black-headed grosbeak and western tanager. Both species sought insects and berries on cutovers. Diversification of habitat caused by cutting the forest in blocks increases the numbers of these birds. Other species that seemingly benefited from logging were olive-sided flycatcher and calaveras and tolmie warblers. Common species not invading logged areas were the wood pewee, hermit warbler, and hammond flycatcher.

Raptors

The red-tailed hawk is a regular visitor about cutovers that support large chipmunk populations. Sharp-shinned hawks frequented the coniferous forest where they nest and, in fall, were often seen about cutovers where they preyed on the flocks of juncos and other small birds. A pair of goshawks (*Accipter gentilis*) nested in one of the virgin forest study areas. Logging benefits the red-tail, and perhaps the sharp-shinned hawk, by breaking up an otheriwse homogeneous habitat and fostering population growth in prey species.

Other species

Many other species were seen about cutover and forest study areas during the investigation. Most of these were not regular inhabitatants and constituted a minor portion of the avifauna of these areas. Most do not eat Douglas-fir seed.

California quail replace mountain quail at low elevations along the important river valleys where they invade logged areas as these become available.

Band-tailed pigeons are common in winter. They sometimes fed in madrone and tan oak trees at the edges of cutovers, but preferred pure stands of these trees, other oaks, and manzanita brush. They ate some Douglas-fir seed during the heavy seed year but did not obtain it from cutovers.

Turkey vultures are very common in summer and were often observed soaring over cutovers. Vultures were once seen feeding on a dead deer on a cutover.

The spotted owl possibly is a rather common bird but individuals were seen only twice, once in daylight in the forest and once after dark hunting around the edges of a cutover.

Screech owls were not counted in any censuses but birds were heard regularly about most logged areas after dark. This species must be at least as common as the sharp-shinned hawk.

Pigmy owls apparently were common in the forest. They seldom were seen but were often heard calling in daytime during April and May.

Ravens sometimes were seen in trees about edges of cutovers.

Lazuli bunting families occupied some of the brush-stage cutovers in summer.

Cassin vireo was a common summer resident in the virgin forest and appeared regularly in trees bordering cutovers.

Hutton vireo (*Vireo huttoni*) was a year-round resident in live-oak thickets. It rarely visits cutovers unless this tree is present.

The Bush-tit was present all year. Flocks of 30 to 35 were seen sometimes on brush-stage cutovers.

Golden-crowned kinglets were common in the virgin forest in winter, where flocks were often heard high in firs.

Townsend solitaire nested on a few high areas, both in the forest and on cutovers, but not regularly. It may be seen at any time of year.

Western bluebirds occasionally were seen on cutovers in late fall and winter.

DISCUSSION

Logging alters the composition of the bird population and may cause a temporary decline in over-all numbers. Within a year after cutting, former numbers are regained, though species composition is different. An increase both in species and numbers of individuals over those in the original mature Douglas-fir forest occurs by the third year after logging. All of the species found on weed-stage (one and 2-year old) cutovers occur in greater numbers on brush-stage (3 to 7-year old) cutovers. The latter carries more birds both in species and numbers than either of the other types.

Juncos, varied thrushes, spotted towhees, mountain quail, golden-crowned sparrows and fox sparrows are the birds that benefit most from logging. These are the important seed eaters of cutovers and are responsible for most of the bird depredation of conifer seeds on the ground. The junco is especially important. Numbers of winter wrens, pine siskins, goldfinches, hairy woodpeckers, California woodpeckers, and robins also increase after logging. Red-breasted nuthatches, chickadees, hermit warblers, and pileated woodpeckers decrease. Some birds, such as the steller jay, may desert a freshly logged area but become more numerous on brush-stage cutovers than in the forest.

Forest birds may become an important hindrance to natural seeding by attacking cones of trees around the edges of cutover blocks. The more important of these are pine siskin, purple finch, red crossbill, red-breasted nuthatch, chestnut-backed chickadee and evening grosbeak.

Actual population size is most easily measured during the breeding season. In 3 breeding seasons the total bird populations averaged 131 pairs per 100 acres on a brush-stage cutover as compared with 119 in a virgin forest study area (Table IV). In Georgia, Johnston and Odum (1956) found 136 pairs per 100 acres in shrubland and 87 to 93 in pine forest.

Juncos use both cutovers and the virgin forest for nesting, but are 2 or 3 times as numerous on brush cutovers as they are on the other 2 types. Other birds found nesting on both cutovers and in the forest were chestnut-backed chickadee, hairy woodpecker, red-breasted sapsucker, black-headed grosbeak, and townsend solitaire. Birds that nested commonly on cutovers but were absent from the forest were mountain quail, spotted towhee, and California woodpecker. The hermit warbler, red-breasted nuthatch, hermit thrush, and pileated woodpecker, all common breeders in the forest, were not found on cutovers at nesting time.

The difference in population size between virgin forest and brush-stage cutover is less during the breeding season and in summer. In fall and winter, the time when Douglas-fir seed is available, birds on the brushy cutovers often outnumber those in the forest by as much as 2 or 3 to one. Spring populations, based on abundance index values for 25 species, were 267 birds per 100 acres on the cutovers and 279 in the forest. Corresponding levels for late fall and winter were 325 and 220 respectively.

How important is depredation by birds on Douglas-fir seed? Conditions of food availability and bird numbers were so greatly different in each of the 3 years of the study that forecasts and generalities would be questionable. Extreme variability in slope, aspect, elevation, and soil in the region are further complicating factors. Successful and unsuccessful seedings were known to occur in different blocks of the same cutting unit.

In a hypothetical situaiton with the junco, it may be conservatively estimated that 40 seeds are consumed per bird per day in late fall and winter of a good seed year. Caged birds consumed Douglas-fir seed at the rate of 180 seeds per day. Junco density on cutovers in the heavy seed year was 1.5 birds per acre. The seeds were available to them on the ground for about 270 days. At these rates, the toll on the crop from juncos alone could have been 16,200 seed per acre. This is 17% of the maximum amount of seed that is likely to fall on a cutover in a good seed year. It should be remembered that the birds concentrated their efforts on the older cutovers.

Control experiments were not a part of this investigation. However, it was found that junco flocks are easily diverted from fir seed by supplying artificial food at just one place on a cutover. As mentioned previously, clearing logs and slash will reduce numbers of seed-eating birds, especially juncos and winter wrens. When making an estimate of the seed potential from a cone crop in Douglas-fir, the forester will do well to note also the size of the other important crops that serve as wildlife food. In the Douglas-fir region, tan oak and madrone are of utmost importance. The size of their crops will greatly influence the degree of bird depredation on fir seed.

SUMMARY

Logging of the forest caused a definite increase in bird population size and a marked change in species composition. There was little change in total number of species at first, but an increase occurred within 3 years after cutting. The junco became predominant on cutovers where an abundance of weed seeds, berries and insects helped the population to flourish. These birds turned largely to Douglas-fir seed when it was available. Other important seed eaters which invade logged areas to forage on the ground were varied thrush, spotted towhee, mountain quail, golden-crowned sparrow, and fox sparrow. Steller jays and winter wrens also were important in the ecology of logged areas, but the former bird was not a harmful influence in Douglas-fir regeneration. Several species of finches, the red-breasted nuthatch, and the chestnut-backed chickadee attacked the cones of seed producing trees around borders of cutovers. Many other species of birds were affected by logging.

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AN ANALYSIS OF BIRD POPULATIONS IN RELATION TO FOREST SUCCESSION IN ALGONQUIN PROVINCIAL PARK, ONTARIO[1]

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Introduction

Algonquin Park is about 150 miles north of Lake Ontario. It is about 70 miles wide and 40 miles in a north-south direction, and consists of rolling, forested terrain with many lakes, rivers and bogs between the hills. It is in the ecotone between the boreal forest and the eastern deciduous forest. Forest succession in the Park has been worked out in detail in another report (Martin 1959). This is an account of the succession of bird populations that accompanied the succession of vegetation.

Briefly, 2 major plant seres were recognized, a hydrosere on wet land and a xerosere on upland. The hydrosere goes from wet bog, to dry bog, to low *Picea mariana* forest, to intermediate *P. mariana*, to high *P. mariana*, to *P. mariana—Thuja occidentalis*, to bottomland forest. The vegetation in the bogs was dominated by *Chamaedaphne calyculata*, and occurred in hillocks. In wet bog the hillocks were separated by water; in dry bog *Sphagnum* and other plants formed a mat over the water, although it was difficult to walk through such an area without breaking through the mat. As the ground-water level dropped and humus was added to the surface, trees of *Picea mariana* appeared, increasing in size as the substratum became less wet. The low *P. marina* forest consisted of clumps of these trees having a diameter at breast height of about 3 in. and a height of about 20 ft. Bog vegetation grew between the clumps. In intermediate *P. mariana* forest, the ground was drier, there were more trees, and these were larger with an average D.B.H. of 5 in. and a height of about 40 ft. There was less bog vegetation here, and *Cornus canadensis*, not found in bogs, was present. In high *P. mariana* forest, the ground was drier than in preceding plots, there were no low-bog shrubs, and the trees were again larger, with an average D.B.H. of 7 in. and a height of about 80 ft. The trees here were close together so that it was difficult to walk through their interlacing lower branches. There were also more species, with *Thuja occidentalis* a conspicuous member. In *P. mariana—Thuja* forest, water stood in pools beneath the tree roots, but the ground-water level was lower than in previous types and the humus was deeper. *P. mariana* was the leading dominant tree, and *Thuja occidentalis* was an important codominant. There was a dense undergrowth of shrubs including *Alnus* sp. and *Viburnum cassinoides*. The top of the canopy was about 80 ft high. The bottomland forest was a mixture of *P. mariana, Thuja occidentalis, Abies balsamea,* and *Betula lutea*, with a dense shrub stratum of *Alnus*. There was no continuous tree canopy in this forest. Individuals of *Abies* reached a height of 30 ft, those of *Picea* a height of 60 ft, and scattered trees of *Betula lutea* grew as high as 80 ft.

The xerosere occurred on upland following fire or cutting. The pioneer forest was dominated by *Betula papyrifera, Populus tremuloides,* and sometimes *Acer rubrum*. Trees of a late stage pioneer forest were about 30 ft high and had a D.B.H. of about 5 in. Usually there was a dense shrub stratum of *Corylus cornuta*. The pioneer forest was replaced by a second stage forest of *Abies balsamea—Picea glauca* in most areas, or by *Pinus strobus* in others. Trees of the *Abies—Picea* forest grew to a height of 50 ft and often occurred in clumps, with grass or thickets of *Corylus cornuta* between the clumps. The *Pinus strobus* forest that was studied was a dense stand of trees about 70 ft high, forming a closed canopy. There was relatively little undergrowth. The third stage in the xerosere was the hardwoods subclimax. This was the *Acer saccharum* facies of the *Fagus—Acer* forest that is well-known in eastern North America. The top of the closed deciduous canopy was 80-100 ft above the ground, and there was usually a prominent shrub stratum of small trees of *Acer*. The climax forest was pure *Tsuga canadensis* (Figure 1). The trees here were about 75 ft high, and there was relatively little growth beneath the dense, closed canopy.

Methods

Plots of about 25 acres each were laid out, usually 2 in each of the seral stages of vegetation, and also in mixed stands which were transitional between successive stages. Censuses of breeding bird populations were taken on these plots in 1952 and 1953. Those plots that were rectangular were divided, using compass and steel tape, into squares 100 ft on the side, and markers were

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[1] Contribution from the Department of Zoology of the University of Illinois.

FIG. 1. Climax *Tsuga* forest.

placed at the corners of the squares. Markers were yellow baggage tags bearing the appropriate orientation information marked with a black grease pencil and nailed in each case to the trunk of the tree nearest to the corner of the squares. Two tags facing opposite directions were used at each corner. Actually, only alternate lines across the plots were measured and marked. In taking a census, the marked lines were traversed and the distance of 100 ft on either side of these lines was determined readily by judgment.

Strip plots were 200 ft wide with a trail or road up the middle. Markers were placed at 100 ft intervals along the middle trail. In taking a census on a strip plot, the middle line was followed, and the distance of 100 ft on either side of the line was determined by judgment.

A map of each respective plot was carried on each census, and as birds were observed, a record of their position, species, sex, distance from the ground and whether singing or not singing was made on the map. Most observations were of singing males, but if a male bird was seen, it was recorded. Females were not noted except in the case of ruffed grouse with young. If a bird's sex could not be distinguished, its presence was recorded.

On each census, a record was made of the time of day and general weather conditions. During June and the first half of July, one census was taken each morning and one each evening. During the second half of July, censuses were taken only in the early morning. An early morning census would last roughly from 7 o'clock to 9, a morning census roughly from 8 o'clock to noon, and an evening census from about 7 o'clock to 9. Virtually no censuses were taken during rain.

At least 5 censuses were taken each year on each plot throughout June and July. At the conclusion of each season census records were collected on plot maps, one for each species for respective plots, and lines were drawn around groups of observations such that all observations within each line represented records of different censuses. These lines were considered to enclose the breeding territories of the nesting male birds. By counting these territories, a determination was made of the breeding density of each species. This is the spot-map method of taking a bird census (Kendeigh 1944).

Where less than half a territory extended inside a plot, the species was represented in the summarizing table with a plus mark. Where territories crossed plot boundaries, proportions of territories inside the plot were summed to give the final density.

Undoubtedly the efficiency of this method varies with the vegetation of the area. In a bog plot, for instance, lack of trees permits most of a bird's movements to be watched, and a relatively exact record of its territory can be made. Where the birds' movements cannot be observed easily, the final territory lines can only be approximated and while this should not affect the determination of breeding density, it confuses the exact outline of a bird's territory. This was borne out in one or two cases where individual birds could be identified by song peculiarities and where the exact

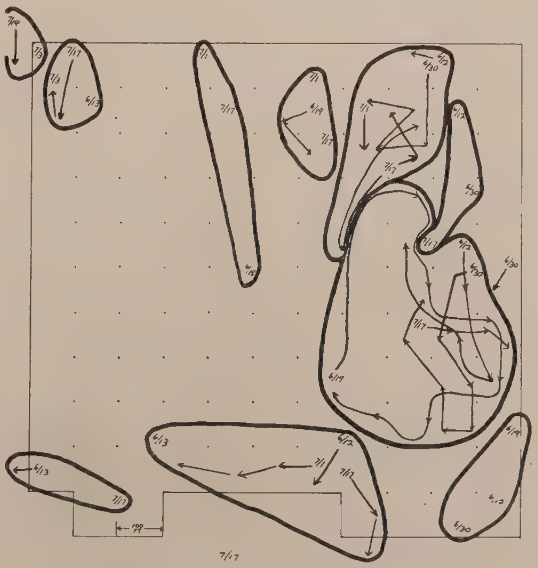

FIG. 2. Nesting territories of the magnolia warbler in *Picea mariana—Thuja* forest, 1952.

territories proved to be decidedly irregular in shape (Figure 2). On the other hand, this does not imply that bird territories are necessarily irregular in shape. Southern and Morley (1950) found that marsh-tits in England had territories of regular shape.

In addition to area, territory has volume (Davis 1942). This was ascertained by estimating the distance from the ground of all birds and nests that were seen. Because the spot-map method of making a bird census does not give the exact territorial boundaries, and the method used here of determining territory depth does not give exact measurements, most of the territorial dimensions presented must be considered as approximations.

Aspection studies of a general character were made in which the movements and activities of the birds were related to the annual cycle of vegetational change. For each species the date of first observation in the spring and as nearly as possible the last observation in the autumn was noted. From May 2nd to July 11th, 1952, a record was made of species that could be heard singing at 6:00 a.m. from outside the cabin where the author stayed on Tea Lake.

RESULTS AND ANALYSIS

Bog

Breeding birds in the bog fell into four main groups (Figure 3): those that inhabited the shrubs and the few scattered small trees, those that inhabited the dead stubs, those with niche including both of these, and one species, the purple finch which moved mostly in the air above the vegetation but nested and fed in the tree-tops on the borders of the bog. The most abundant, swamp sparrow, yellow-throat, and song sparrow (Table I), belonged to the first group. The territories of the swamp sparrow and yellow-throat were small (Table II) and tightly packed together. Birds of the stubs included the kingbird, tree swallow, alder flycatcher, and olive-sided flycatcher; birds that occurred in both were the yellow-shafted flicker, cedar waxwing, red-winged blackbird, and grackle. The purple finch spent much of its time in the air high above the ground. It was observed at heights up to 150 ft.

Species that were found in the bog but not in any other stage of the hydrosere (Table I), xerosere (Table III), or in forest border (Table IV) included the red-winged blackbird, kingbird, black duck, alder flycatcher, and American bittern. While the tree swallow and barn swallow appear in the tables only under bog, they were also found feeding in other communities.

TABLE I. Territorial males per 100 acres in hydrosere (average of 1952 and 1953)

Species	Wet Bog (Plot B 1)	Dry Bog (B 2)	*Picea mariana* (S 2)	*P. mariana —Thuja* (S 1)
Barn swallow	†			
Black duck	4			
Alder flycatcher	4			
Bronzed grackle	2	3		
Red-winged blackbird	12	3		
Kingbird	9	8		
Tree swallow	14	7		
Song sparrow	16	27		
Swamp sparrow	176	91		
Purple finch	2		2	2
Yellow-shafted flicker	4	6	†	†
Cedar waxwing	4	3	4	6
Yellow-throat	40	134	26	2
American bittern		†		
Olive-sided flycatcher		2		2
Blue jay			†	
Ruffed grouse			2	
Yellow-bellied sapsucker			2	
Canada jay			2	2
Brown creeper			†	4
Black and white warbler			2	4
Blackburnian warbler			2	4
Slate-colored junco			6	2
Black-capped chickadee			2	7
Northern water-thrush			9	2
Olive-backed thrush			4	8
Canada warbler			†	12
Myrtle warbler			5	8
Winter wren			7	8
Golden-crowned kinglet			12	7
Magnolia warbler			4	27
Arctic three-toed woodpecker				†
Scarlet tanager				†
Ruby-crowned kinglet				2
Chestnut-sided warbler				2
Red-breasted nuthatch				4
Spruce grouse				6
Veery				6
Territorial males	287	284	189	225
Principal species present	12	10	20	25
Total species present	13	11	24	28

† The species has been recorded at least twice.

Picea mariana *Forest*

With its scrub trees, the *Picea mariana* forest had more bird species than did the bog. Eighty-three % of the species here were not found in bog, while 66% of the bog species were not found here. The white-throated sparrow, which was not present in the earlier stage of succession, was most abundant. The yellow-throat, which was the most abundant species in dry bog, was in second place with a density of a fifth that of the dry bog. The yellow-bellied flycatcher and Nashville warbler, neither of which was present in the bog, were third in abundance here. The swamp sparrow and the song sparrow were not present, the former probably in response to the absence of water on the surface of the ground, the latter to the forested nature of this plot. There were no exclusive species in this forest type.

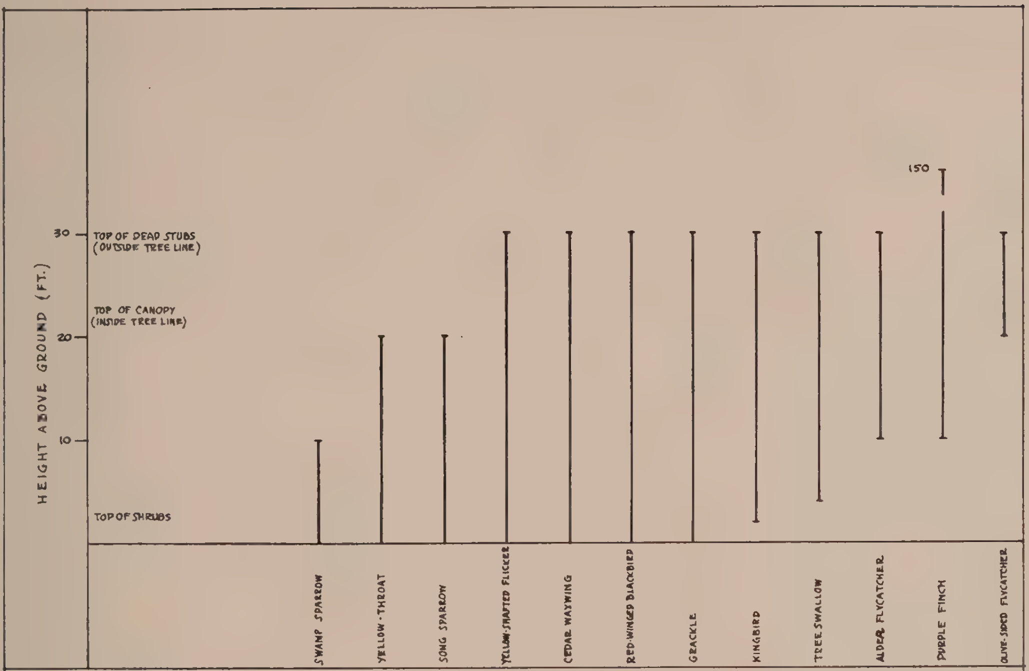

FIG. 3.

Fig. 3. Depth of bird territories in plots B 1 (wet bog) and B 2 (dry bog).

Picea mariana—Thuja *Forest*

Here there was an increase in the species of trees over the previous area, and trees were larger than in the pure *P. mariana* forest. The white-throated sparrow was again the most abundant bird, but with a lower density which may be a negative response to the denser and higher canopy of the *P. mariana—Thuja* stand. The Nashville warbler was second and the magnolia warbler third, both with greater densities than in *P. mariana* and probably both in response to the drier conditions in the *P. marina—Thuja* stand. The yellow-throat, on the other hand, was barely represented, possibly because of the much less open nature of the forest. There were no territorial species exclusive to this forest type. As in other plots, bird territories showed vertical stratification (Figure 4).

Summary of the Hydrosere

Although there were half as many breeding species in the bog plots as in the 2 forested plots, the population of breeding birds was higher in the 2 bog plots because 2 species, swamp sparrow and yellow-throat, occurred in great density there. In fact the density of either of these species was greater than that of any other species in any plot studied. Otherwise the breeding population was low in the bog, as might be expected from the virtual absence of a tree stratum.

The *P. mariana* forest probably had a low population because the vegetation was relatively uniform throughout most of the plot. The ground was covered with *Sphagnum*, there was a low-shrub stratum of ericaceous plants, and the trees were virtually restricted to one species.

The *P. mariana—Thuja* had a higher bird population with the largest number of species. Its ground stratum was diversified with fallen logs, its high-shrub stratum was well developed with *Alnus* and similar shrubs, and its tree stratum included several species of conifers of various heights, with many dead stubs. Thus it had more niches present than did the other stages.

Betula—Populus *Forest*

In this pioneer deciduous forest the oven-bird was the most abundant species, red-eyed vireo second, and veery third. Only the black-billed cuckoo was found nesting exclusively here, although it may have nested as well in deciduous forest border. The birds appeared to fall into 5 principal groups (Figure 5): those that occupied the ground and shrubs (ruffed grouse, slate-colored junco), those with activities extending upward to the lower tree branches (veery, Canada warbler, white-throated sparrow, oven-bird,

Table II. Territory dimensions of bird species for which at least ten records were available

Species	Area (acres)			No. of area records	Depth (ft.)	Volume (av. area x depth)
	Average and standard deviation	Max.	Min.			(cu. meters)*
Ruffed grouse....	1.49±1.27	3.93	0.24	10	10	4,081
Yellow-bellied sapsucker.....	1.61±2.01	6.75	0.15	15	33	14,595
Yellow-bellied flycatcher....	0.65±0.53	2.31	0.09	22	25	4,478
Least flycatcher..	0.32±0.24	0.93	0.08	10	10	878
Black-capped chickadee.....	1.27±0.90	4.0	0.18	33	26	9,069
Red-breasted nuthatch.....	1.22±1.06	3.2	0.2	12	34	11,393
Winter wren.....	1.22±0.87	2.90	0.15	14	14	4,704
Robin...........	2.59±2.28	7.48	0 26	16	54	38,457
Hermit thrush...	1.93±1.80	8.35	0.15	23	38	20,150
Olive-backed thrush.......	2.37±3.32	12.71	0.30	12	20	13,036
Veery...........	0.67±0.59	2.70	0.10	61	23	4,223
Golden-crowned kinglet.......	0.84±0.75	3.2	0.22	20	22	5,073
Red-eyed vireo...	0.46±0.35	1.52	0.06	139	36	4,563
Black and white warbler......	1.29±1.53	6.86	0.05	22	39	13,830
Nashville warbler.	0.92±0.84	5.9	0.06	45	40	10,117
Magnolia warbler.	0.75±0.81	4.18	0.06	68	25	5,578
Black-throated blue warbler..	1.68±1.18	3.83	0.25	11	29	13,358
Myrtle warbler...	1.17±1.09	4.5	0.13	41	38	12,214
Black-throated green warbler.	0.64±0.82	5.38	0.02	49	51	8,984
Blackburnian warbler......	0.44±0.49	2.38	0.1	79	40	4,846
Chestnut-sided warbler......	0.37±0.26	1.25	0.10	41	24	2,437
Oven-bird.......	0.58±0.54	4.0	0.06	143	25	3,996
Yellow-throat....	0.34±0.26	1.59	0.06	95	16	1,502
Canada warbler..	0.55±0.37	1.96	0.15	47	14	2,125
Redstart........	0.36±0.32	1.83	0.07	56	29	2,862
Red-winged blackbird.....	1.19±1.57	6.95	0.09	23	30	9,806
Slate-colored junco........	1.29±0.99	3.6	0.21	19	49	17,372
White-throated sparrow......	0.52±0.48	2.7	0.05	110	17	2,437
Swamp sparrow..	0.36±0.24	1.24	0.05	82	10	992
Song sparrow....	1.07±0.68	2.54	0.15	24	20	5,895

* 28.35 cu. meters = 1 cu. rd.

redstart, black-throated blue warbler); those which were active from the ground or near it roughly to the tree tops (red-breasted nuthatch, black and white warbler, Nashville warbler, robin, hermit thrust, chestnut-sided warbler, red-eyed vireo, yellow-bellied sapsucker, magnolia warbler, myrtle warbler, least flycatcher, and black-throated green warbler); the cedar waxwing that was only seen in the canopy; and the purple finch with territory extending 150 ft from the ground.

Betula—Populus *and* Abies—Picea

With the intrusion of *Abies* and *Picea* into the pioneer forest (Plot BS-PB), the oven-bird remained the predominant species, but with a lower density than in *Betula—Populus*. The red-eyed vireo also had a lower density, while the magnolia warbler, a coniferous forest species, had a density just as great as the red-eyed vireo's. The white-throated sparrow, in response to the presence of conifers, was fourth in abundance, while the veery, a deciduous forest species, had a density lower than in *Betula—Populus*.

A stratification of bird species occurred with the olive-backed thrush, white-throated sparrow, Canada warbler, black-capped chickadee, and veery remaining in the shrubs and lower branches of the conifers. Yellow-bellied sapsucker, blue-jay, and Nashville warbler were not seen above a height of 30 ft; the last 2 usually occupied the conifers, the sapsucker the trunks of deciduous trees. Hermit thrush, black and white warbler, magnolia warbler, blackburnian warbler, golden-crowned kinglet, and myrtle warbler were not seen above 40 ft, which represented the top of the coniferous forest canopy. Robin and red-eyed vireo, both deciduous forest birds, were active in the overstory of deciduous foliage.

Abies—Picea *Forest*

Here the white-throated sparrow, magnolia warbler, and myrtle warbler were most abundant; the oven-bird, red-eyed vireo, and veery were not recorded. The birds could be divided into those with niches (and consequently territories) extending to the ground and those with niches which did not. These groups could be divided again into those that occupied the shrubs and lower tree foliage (ruffed grouse, spruce grouse, white-throated sparrow, and golden-crowned kinglet), and those that occupied the central canopy (flicker, Canada jay, blue-jay, chestnut-sided warbler, redstart, magnolia warbler, yellow-bellied flycatcher, myrtle warbler, blackburnian warbler, and ruby-crowned kinglet). The position of the golden-crowned kinglet in the lower part of the canopy differs from that of some other areas (Bent 1949), but the species rarely was seen near the tree tops in any community in the Park. Black-capped chickadee, black and white warbler, Nashville warbler and junco were active from ground to tree tops and the cedar waxwing from top of shrubs to top of trees. The purple finch spent considerable time in the air over the forest.

Immature Pinus strobus

When the secondary forest was *Pinus strobus* instead of *Abies—Picea*, the oven-bird maintained the predominance it had in the pioneer forest. Black-capped chickadee was second, and red-breasted nuthatch and slate-colored junco were

TABLE III. Territorial males per 100 acres in the xerosere (average of 1952 and 1953)

Species	*Betula—Populus* (Plots PB 1, PB 2)	*Betula—Populus* and *Abies—Picea* (BS-PB)	*Abies—Picea* (BS)	*Immature Pinus strobus* (P 1)	*Abies—Picea* and hardwoods (BS-H)	Hardwoods (H 1, H 2)	*Tsuga* (He 1, He 2)
Crested flycatcher	†						
Yellow-bellied flycatcher	†		3				
Chestnut-sided warbler	16	†	17		14		
Canada warbler	16	14	†		23		
Black-billed cuckoo	1					†	
Ruffed Grouse	6		6		6	†	
Rose-breasted grosbeak	†				†	4	
Least flycatcher	1					6	
Blue jay	†	3	3*	2	†	†	
Black-throated blue warbler	1			†	3	4	
Scarlet tanager	1				3	4	
Cedar waxwing	2		8			†	
Robin	2	3			3	2	
Yellow-bellied sapsucker	2	6	†		3	6	
Redstart	18	†	3		18	11	
Veery	22	9			18	12	
Pileated woodpecker	†						1*
Hairy woodpecker	†				†	†	3*
Yellow-shafted flicker	1		3*	†			2
Purple finch	1	†	8	†	3	†	3
Hermit thrush	10	6		†		†	5
Slate-coloured junco	3	†	3	4			13
Nashville warbler	2	6	6		9		3
Black and white warbler	2	8	3		17		5
Black-capped chickadee	4	6	6	6	6	4	14
Black-throated green warbler	3				6	20	28
Myrtle warbler	1	6	36	3	6		17
White-throated sparrow	4	15	56	1	8		9
Magnolia warbler	1	17	41		31		9
Red-eyed vireo	27	17			20	49	17
Blackburnian warbler	†	8	5	3	15		102
Oven-bird	42	25		20	33	30	2
Bronzed grackle		†					
Ruby-throated hummingbird		3					
Golden-crowned kinglet		7	18				2
Spruce grouse			3				
Song sparrow			6*				
Yellow-throat			6		6		
Canada jay			3				†
Ruby-crowned kinglet			6				†
Brown creeper				1		2	7
Red-breasted nuthatch				4	3	1	10
Wood thrush					3	3	
Olive-backed thrush					1		3*
Wood pewee						4	
White-breasted nuthatch						4	
Downy woodpecker						2	2
Broad-winged hawk							1*
Barred owl							1*
Bay-brested warbler							1*
Blue-headed vireo							2
Chipping sparrow							2*
Winter wren							5
Parula warbler							5
Territorial males	189	159	249	44	258	168	274
Principal species	25	17	22	9	24	18	28
Total species present	32	22	24	13	27	25	30

* Found commonly in other communities in other areas.
† The species has been recorded at least twice.

third in the study area. The forest had a shallow canopy high above the ground. Three species remained in the canopy, and 6 remained below it.

In addition to the species found on the census area, evening grosbeaks, red and white-winged crossbills, pine siskins, and purple finches often were seen and heard flying over the forest.

Abies—Picea *and Hardwoods*

As in the deciduous forests of earlier seral stages, the oven-bird was here the most abundant

Table IV. Territorial males per 100 acres in forest border plots, and in plots other than border showing the highest density in 1953

Species	Border 1 (Plot E 1)	Border 2 (E 2)	Plots Other Than Forest Border With Highest Density	
			Plots	Density
Ruffed grouse	†		PB, BS, BS-H:	6
Black-billed cuckoo		†	PB:	1
Ruby-throated hummingbird	4		BS-PB:	3
Yellow-shafted flicker	4	4	B2:	6
Yellow-bellied sapsucker	4	†	BS-PB, H:	6
Hairy woodpecker		†	He:	3
Kingbird		†	B1:	9
Crested flycatcher		†	PB:	†
Yellow-bellied flycatcher	4		S1:	22
Alder flycatcher		†	B1:	4
Least flycatcher	†	4	Edge of H:	6
Wood pewee	4		H:	4
Olive-sided flycatcher	†		B2, S1:	2
Canada jay	†		BS:	3
Blue jay	4		BS-PB, BS:	3
Black-capped chickadee	4	12	He:	14
Red-breasted nuthatch	†		He:	10
Brown creeper	†		He:	7
Winter wren	4		S1:	8
Catbird		†	—	—
Robin	20	15	BS-PB, BS-H:	3
Wood thrush	†		BS-H, H:	3
Veery	12	20	PB:	22
Golden-crowned kinglet	†		BS:	18
Cedar waxwing	3	8	BS:	8
Starling		†	—	—
Red-eyed vireo	40	10	H:	49
Black and white warbler	8	†	BS-H:	17
Nashville warbler	12	5	S1:	28
Parula warbler	†		He:	5
Magnolia warbler	27	4	BS:	41
Black-throated blue warbler	11		H:	4
Myrtle warbler	8		BS:	36
Black-throated green warbler	8		He:	28
Chestnut-sided warbler	3	25	BS:	17
Blackburnian warbler	16		He:	102
Oven-bird	20	11	PB:	42
Northern water-thrush	†		S2:	9
Mourning warbler	†	10	—	—
Yellow-throat	†	18	B2:	134
Canada warbler	12	12	BS-H:	23
Redstart	12	26	PB, BS-H:	18
Red-winged blackbird		†	B1:	12
Rusty blackbird	†		—	—
Scarlet tanager	7		H:	4
Rose-breasted grosbeak	3		H:	4
Indigo bunting	8	7	—	—
Evening grosbeak	†		—	—
Purple finch	4	1	BS:	8
Slate-colored junco	7	4	He:	13
Chipping sparrow	†		He:	2
White-throated sparrow	20	8	S2:	62
Swamp sparrow		4	B1:	176
Song sparrow		26	B2:	27
Territorial males	293	234		
Principal species present	29	21		
Total species present	44	31		

† Indicates the species has been recorded at least twice.

species. The magnolia warbler was second but with a lower density than in pure coniferous forest, and the Canada warbler was third. The birds fell into 4 general groups according to the height above the ground to which they were active: those of the shrubs and lower tree branches, those that did not go above 30 or 40 ft, those that extended to the top of the main canopy (65 ft), and the purple finch occupying the crowns of the tallest trees and the air above them as well as all other heights down to the ground.

Hardwoods

In the hardwood forest of *Acer saccharum* and *Betula lutea*, the red-eyed vireo was most abundant, the oven-bird was second, and the black-throated green warbler third. Most of the birds lived below the main tree canopy (Figure 6), within a lower stratum of abundant second growth. Only the scarlet tanager was found frequently at the top of the canopy, although a few other species were sometimes active within it.

Tsuga *Forest*

In this, the climax forest, the blackburnian warbler was most abundant, black-throated green warbler second, and red-eyed vireo and myrtle warbler third. Only 4 species were found above a height of 60 ft, and 2 of these were the 2 most abundant (Figure 7).

Summary of the Xerosere

The breeding species in the xerosere appeared to show a primary selection for coniferous or deciduous forest. There was an alternation of deciduous and coniferous forests resulting in an early deciduous stage, early coniferous stage, late deciduous, and late coniferous stages, and there was some evidence of secondary selection by the birds for the early or late stages. This may have been a response to the height of the forest. In the early stages, the forest canopy was relatively low; in the later stages it was high with a deep stratum of tree trunks.

The low population in immature *Pinus strobus* might be explained on the basis of the uniformity of this type of forest. However the *Tsuga* forest, with the greatest breeding density and number of species, was also a fairly uniform forest; in fact its physical structure was similar to that of the *Pinus* stand, with a litter of needles, few herbs and shrubs, and a continuous coniferous canopy. The *Betula—Populus* associes, with a fairly diversified physical structure, had a relatively low breeding population, although a good representation of species. It appears that the coniferous plots supported a higher breeding population, although not necessarily a greater number of species, than the deciduous plots.

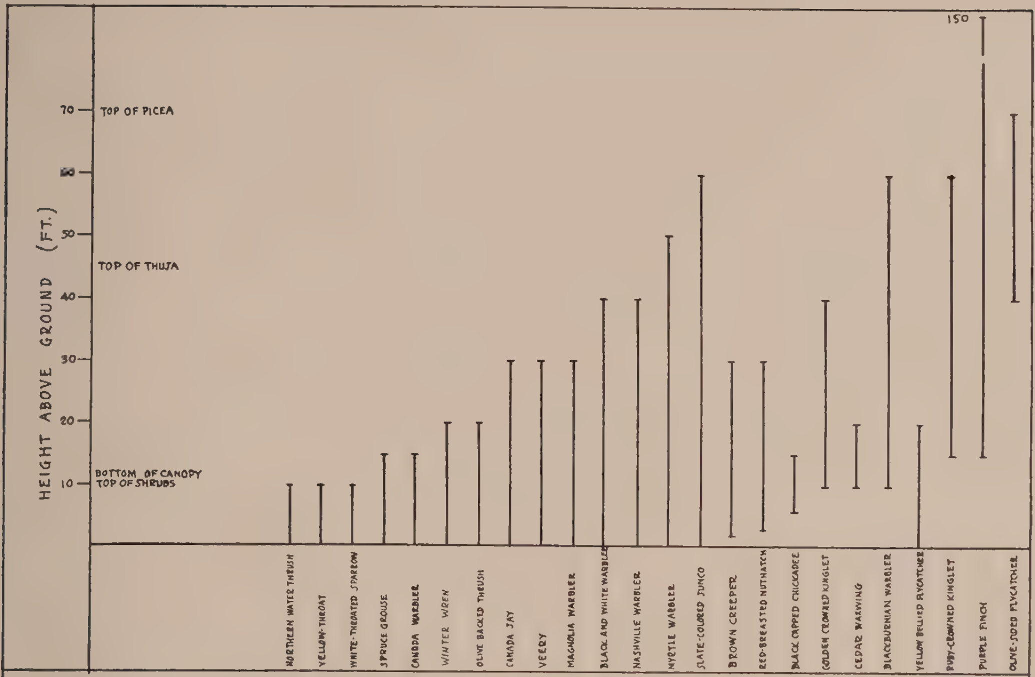

FIG. 4.

FIG. 4. Depth of bird territories in plot S 1 (*Picea mariana—Thuja*).

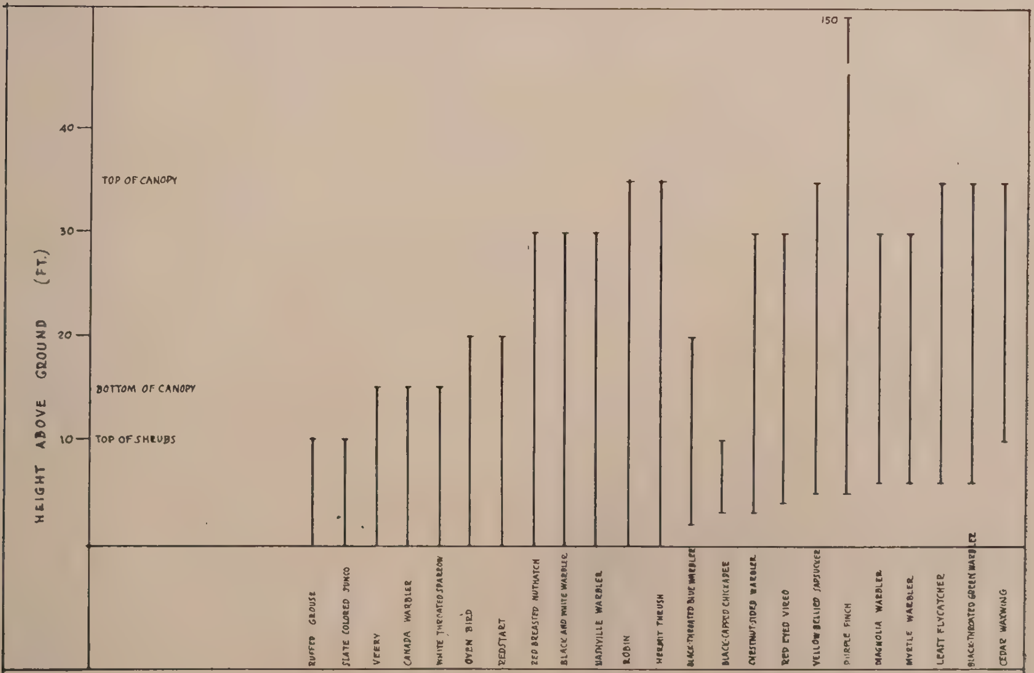

FIG. 5.

FIG. 5. Depth of bird territories in plots PB 1 and PB 2 (*Betula—Populus*).

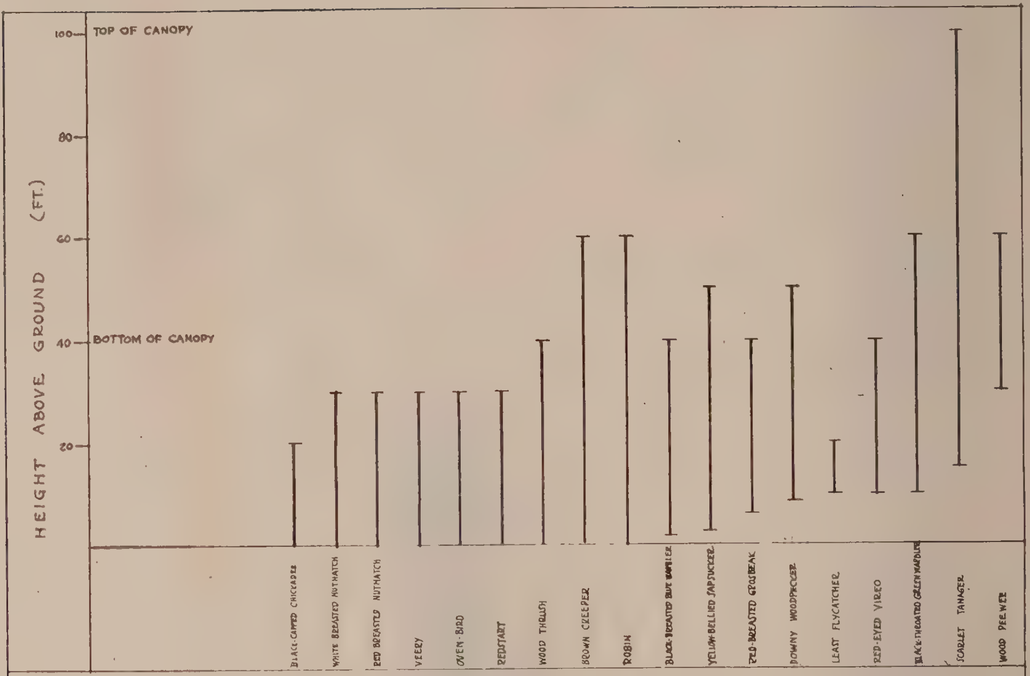

FIG. 6.

FIG. 6. Depth of bird territories in plots H 1 and H 2 (hardwoods).

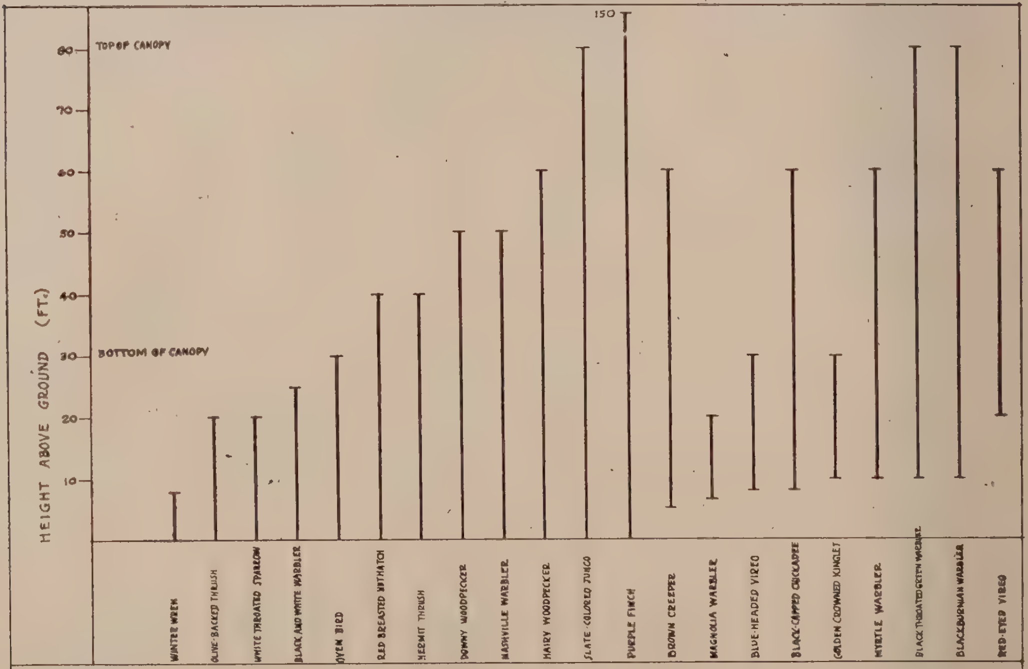

FIG 7.

FIG. 7. Depth of bird territories in plots He 1 and He 2 (*Tsuga*).

Forest Border

Plot E 1 was border to mixed coniferous and deciduous forest, Plot E 2 was border to *Betula—Populus* forest and bog. In the first, the red-eyed vireo, a deciduous forest species, was most abundant. The magnolia warbler, a coniferous forest species, was second. Both these species had higher densities in plots other than E 1. Robin, oven-bird, and white-throated sparrow were third. Of these the robin had its maximum density in the border, the oven-bird in *Betula—Populus,* and the white-throated sparrow in *Abies—Picea.* In plot E 2 the redstart and song sparrow were the most abundant species, the chestnut-sided warbler was second and the veery third. The redstart and chestnut-sided warbler were more abundant here than elsewhere; the song sparrow was more abundant in bog, and the veery in *Betula—Populus.* There was a larger variety of species in the border of coniferous-deciduous forest than of *Betula—Populus*—bog. Undoubtedly there was much penetration of species from neighboring vegetation types in both plots.

The border plots had high breeding populations with a large number of species. Of the 54 species recorded as occurring in the border plots, however, only 14 had a higher density than in any other plot, of which 6 were recorded exclusively in forest border. Two species were found in equal density in forest border and in some other plot, and 38 of the birds recorded in forest border were recorded in higher densities elsewhere. This suggests that the forest border plots had a high density of birds because they attracted a relatively large number of species, but for most species they probably did not provide optimum breeding habitat.

Territories

Territories are three-dimensional and have volume as well as area. Dunlavy (1952) suggests that the vertical movement of birds varies with species. The depth of a territory is often so small relative to the length and breadth that the volume may be chiefly a function of the horizontal dimensions, but an accurate conception of territory should consider its depth. In Algonquin Park there was little evidence of males defending territories from intruders from above or below, but the top of the canopy in the Park is rarely over 100 ft high. It is conceivable that in a higher and more complex forest territories could be defended vertically as well as horizontally.

Niche Characteristics

In most cases birds occurred where they did in order to satisfy niche requirements. Song-posts were usually located at the tops of the territories, often on conspicuous perches where rival males would be notified with the greatest efficiency. In contrast, nests of most species were at or near the bottoms of the territories—on the ground or in the shrub stratum. Only a few species nested in the tree canopy. This may reflect a greater predation pressure from hawks, owls, and crows, than from such animals as skunks, foxes, mink, and marten, on or near the ground. While most of the birds were found eating a variety of small invertebrates, they were seen most often with caterpillars (Lepidoptera) collected from the foliage of shrubs and trees.

Aspection

Aspects were well-marked. The hiemal aspect extended roughly from the first of December to the end of March. During this time the ground was covered with snow which attained a depth of about 40 in. in late February. During December the lakes froze over. The permanent resident birds at this season appeared to prefer coniferous forest and coniferous forest border, possibly because conifers provided food in their cones for the seed-eating species, and shelter from wind and predators. Various species, particularly the grosbeaks, were often found on the ground along the highway where they appeared to be attracted by salt which was thrown there by road maintenance authorities. Jays fed on insects in cocoons which they obtained by stripping off the bark of decaying trees. Nuthatches and woodpeckers worked over the trunks of trees. Grouse were seen in the foliage of *Tsuga* 20 ft above the ground, apparently eating seeds and needles. Chickadees searched through the foliage of conifers and the twigs and loose bark of deciduous trees. Purple finches, redpolls, and crossbills fed on seeds at the tops of *Picea* spp. Ravens fed on the carcasses of dead animals. Most birds appeared to range the countryside widely, and fed in the afternoons often until it was too dark to identify them.

During the latter half of March the temperature was often above freezing during the day and by the end of March the snow had melted from much of the ground. Although there was some tendency for south slopes to be free from snow before north slopes, the snow melted rapidly from all exposures, and the aspect changed from hiemal to prevernal fairly suddenly compared with disstricts south of the Laurentian Shield.

The prevernal aspect lasted through April. As patches of ground became clear of snow, some birds, such as chickadees, nuthatches, and jays moved down onto them to feed. Throughout April the weather was alternately sunny and warm, and cold and raw. The forest was quiet as far as bird songs were concerned. Winter residents and migrant species (including Canada geese) were moving north in flocks, and early summer residents were returning. Ground vegetation was still flattened by the recently melted snow.

At the end of April the aspect changed from prevernal to vernal. The vernal aspect continued to the end of May. The leaves opened, the warblers and most other birds returned, set up territories, and mated. The aestival aspect lasted through June and July. In June, nights were cool and days warm or hot. The last bird arrivals appeared, and most species were nesting. During the first half of June most species had eggs, and, during the latter half, young in the nests. During July, parent birds fed young out of the nest, and singing became restricted to early morning and late evening. By the end of the month, territorial boundaries were breaking down.

A record of the number of species heard singing at 6 a.m. during the breeding season of 1952 (Figure 8) gives some indication of seasonal change from vernal to aestival aspect.

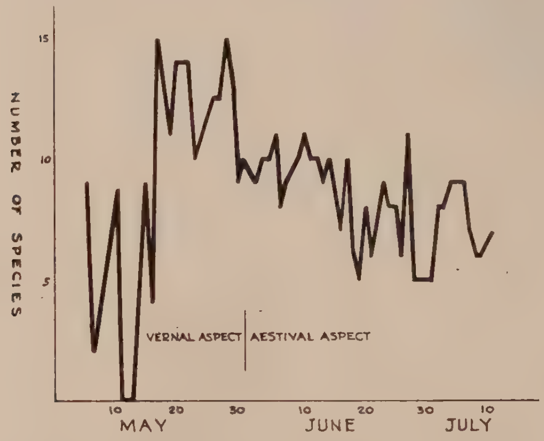

Fig. 8. Number of species heard singing in hardwoods —*Abies*—*Picea*—forest border from 6.00 to 6.05 a.m. spring, 1952.

The serotinal aspect lasted through August. Birds became silent and retiring, family groups broke up, and moulting individuals were often seen. Birds appeared to search for food during the morning and became inactive in the afternoon. White-throated sparrows were flocking on August 15th, and throughout the month migrating shore birds were seen on mud flats. Calls of migrating birds were heard at night.

At the end of August flocks of migrating warblers appeared, and the autumnal aspect began. Throughout September flocks of sparrows passed through. During the first half of October leaves changed color and fell, Canada geese passed over, flocks of thrushes went through, and migrating ducks began to appear. Song sparrows, nuthatches, and blue jays were seen feeding until well into dusk. During the latter half of the month, migration of summer residents was mostly completed except for ducks. Winter residents appeared. In November duck migration was completed, and forests were relatively silent.

Discussion

Bird Communities

It is evident (Tables I, III) that there is a succession of birds in Algonquin Park as well as of forest types, but every plant stage does not necessarily include a distinct community of birds (Kendeigh 1948). In order for 2 populations of birds to be considered separate communities, each population should have at least 50% of its species characteristic for its particular habitat. The 50% level is significant because it is the turning point beyond which 2 populations of species become more different than they are alike. When differences between 2 populations are below the 50% level, they may be considered as *facies* of the same community.

It becomes necessary then to determine the preferences of species for particular forest types for which they may be considered characteristic. This preference may be indicated by the difference in population densities attained by the species. Populations may vary in size because of the influence of factors other than preference but such variability is usually inversely proportional to size. In this study, when the population of a species is not more than 10 pairs per 100 acres in either of 2 forest types, it is considered to show preference and be characteristic of one if its density there is at least 3 times what it is in the other. Likewise when the population density of a species is over 10 pairs per 100 acres in one or both forest types it is considered as showing preference for one if it is at least 2 times as abundant in it as in the other. Definite preference for one community over another is believed not to be indicated when the difference in population levels is not of these orders of magnitude. This is a matter of judgment but is conservative, since known sources of error in the spot-map method of censusing standing populations is approximately ± 10%. With species having 2 broods per year there may be a disappearance of some birds and influx of new birds between nestings that is not detected so that the error of censusing of the cumulative population may be off as much as 25% (Fawver 1950). Table V gives comparisons be-

TABLE V. Determination of bird communities

Plant communities compared	No. of species	% of species showing preference
Betula—Populus	25	48
Betula—Populus—Abies—Picea	17	59
Betula—Populus—Abies—Picea	17	47
Abies—Picea	22	77
Betula—Populus	25	52
Abies—Picea	22	73
Betula—Populus	25	44
Hardwoods	18	72
Abies—Picea	22	55
Abies—Picea—hardwoods	24	62
Abies—Picea—hardwoods	24	54
Hardwoods	18	44
Abies—Picea	22	91
Hardwoods	18	94
Abies—Picea	22	82
Pinus	9	33
Abies—Picea	22	68
Tsuga	28	68
Pica mariana	20	30
P. mariana—Thuja	25	40
Picea mariana—Thuja	28	46
Abies—Picea	22	45
Picea mariana—Thuja	28	54
Tsuga	28	64
Hardwoods	18	72
Tsuga	28	86
Forest border	33	12
Forest interior	52	54
Wet bog	12	42
Dry bog	10	20
Bog	13	69
Forest border	34	82
Betula—Populus	25	12
Forest border	34	41

tween several pairs of plant communities in respect to preferences shown by species for one or the other.

It is apparent that the *Abies—Picea* and hardwoods plant communities contain distinct bird communities, while mixtures of these 2 plant communities or of either of them with *Betula—Populus* contain mixtures, or ecotones, of their respective bird communities. The status of *Betula—Populus* as a distinct bird community is open to question. It contains a mixture of birds from both coniferous and deciduous forest. The 2 most abundant species in *Betula—Populus*, oven-bird and red-eyed vireo, are also the most abundant in hardwoods. On the other hand, of the 7 species in *Betula—Populus* that were found in a density of 10 or more territorial males per 100 acres, 4 should be considered as characteristic of this forest—redstart, chestnut-sided warbler, Canada warbler, and hermit thrush. It may be argued that *Betula—Populus* is really a form of forest border. Floristically this is untenable; the *Betula—Populus* forest and its facies presented a relatively uniform and simple composition in all strata, whereas forest border was varied and complex. As far as birds are concerned, it does not seem reasonable to subjugate a community that occurs over extensive areas to one that occurs over relatively limited areas under the special conditions that produce a border. As far as this study is concerned, *Betula—Populus* (which should be called pioneer deciduous forest in order to include its several facies) appears to be a borderline case.

Pinus and the hydroseral forests of *Picea mariana* and *P. mariana—Thuja* have essentially the same birds as *Abies—Picea*. These forests (excepting *Pinus*) may be called the boreal forest community. *Tsuga* forest and bog hold distinct bird communities. It is not possible to compare coniferous forest border and deciduous forest border, since these types were not separated when the plots were laid out. Birds of forest border, including borders of coniferous forest, deciduous forest, various mixtures of these, and bog, do not form a community distinct from forest interior, but do form a community distinct from bog.

As a result of this analysis, the following may be considered as containing distinct bird communities:

1. bog
2. boreal forest
3. *Tsuga*
4. deciduous forest

Characteristic birds of these communities in this region are:

Bog

swamp sparrow
yellow-throat
tree swallow
red-winged blackbird
kingbird
black duck
alder flycatcher
bronzed grackle

Tsuga

blackburnian warbler
black-throated green warbler
red-breasted nuthatch
brown creeper
slate-colored junco
parula warbler
chipping sparrow
bay-breasted warbler
blue-headed vireo

Boreal forest

white-throated sparrow
magnolia warbler
myrtle warbler
golden-crowned kinglet
yellow-bellied flycatcher
cedar waxwing
spruce grouse
ruby-crowned kinglet
Canada jay
northern water-thrush

Deciduous forest

red-eyed vireo
oven-bird
veery
scarlet tanager
black-throated blue warbler
rose-breasted grosbeak
wood thrush
wood pewee
white-breated nuthatch

Pioneer facies
deciduous forest
redstart
chestnut-sided warbler
Canada warbler
hermit thrush
black-billed cuckoo
whip-poor-will

The whip-poor-will was not encountered on censuses, but singing males were heard almost invariably in pioneer decidous forest.

Kendeigh (1948) found the white-throated sparrow to be a coniferous forest border species in Michigan. In Algonquin Park this species showed preference for boreal forests of *Picea mariana, P. mariana—Thuja* (Table I), and *Abies—Picea* (Table III). While the trees in *Picea mariana* were relatively small in parts of the plot and *Abies—Picea* included many small openings, *P. mariana—Thuja* could not be construed as a form of border. It was a dense forest, with the white-throated sparrow often most abundant in the densest parts. The density of territorial males in any of these plots exceeded that of either of the forest border plots (Table IV), although there was no plot of entirely coniferous forest border.

Succession

Corresponding with the succession of plant communities (Martin 1959), the succession of bird communities is as follows:

Tsuga
↑
deciduous forest
↑
boreal forest
bog ↗ ↖ pioneer facies of deciduous forest

As with tree species, there is an intergrading of bird species from one forest type to another and it is difficult to eliminate a subjective element in the recognition of distinct communities. The dominance of certain tree species seems to modify and determine the whole biotic character of respective forest stands, although the ornithological content of these stands may be more flexible than the vegetation. While the oven-bird was one of the most abundant species in deciduous forest, it was also one of the most abundant in *Pinus strobus,* even in the absence of much deciduous undergrowth. The black-throated green warbler was characteristic of *Tsuga,* but was also found in hardwoods with no *Tsuga* present, as Kendeigh (1946) found at high altitudes in New York. No nests of this warbler were found in either forest, but Bent (1953) notes that nests have been found in both coniferous and deciduous vegetation. A few birds show well-marked community preferences, but many others tend to be cosmopolitan. There is little doubt that birds occur where their niche requirements are satisfied, other factors such as competition being equal, but for most species these requirements need yet to determined.

There is no doubt, however, that the bird communities are differentiated as distinct facies in each forest type. It is possible to distinguish one forest type from another simply by listening to the singing birds. The presence of certain combinations of birds, their relative abundance and conspicuousness, and their vertical distribution characterize each stage of forest succession that was studied.

Bog is readily identified by the predominance of the swamp sparrow and yellow-throat, and dry bog can be distinguished from wet bog by the general distribution of the yellow-throat and the localized distribution of the swamp sparrow, which in wet bog is just the reverse. *Picea mariana* forest can be identified by the predominance of the yellow-throat and white-throated sparrow, the relative scarcity of other species, and often the presence of the olive-backed thrush, which, though not as abundant as in some stands, may have a high degree of conspicuousness. In *P. mariana—Thuja* forest, the white-throated sparrow is conspicuous and the magnolia warbler is abundant and usually singing close to the ground. In addition, the yellow-bellied flycatcher is almost diagnostic. In *Abies—Picea* forest the magnolia warbler usually sings from high in the trees. The myrtle warbler, which is scarcely noticeable in *P. mariana—Thuja,* is abundant and sings from mid-canopy. The purple finch is usually present at the tree-tops or in the air overhead. The yellow-bellied flycatcher is scarce and inconspicuous.

In *Betula—Populus* the oven-bird and red-eyed vireo are abundant and close to the ground. In addition the redstart and chestnut-sided warbler are abundant. In hardwoods, the birds are spread over a greater vertical distance and are consequently less conspicuous. The red-eyed vireo commonly sings from the canopy, the oven-bird sings from well up in the shrub stratum, the redstart is confined to clearings, and the chestnut-sided warbler is absent. As in most forest-types, there are certain almost diagnostic species. In *Betula-Populus* the hermit thrush is one of the most conspicuous of these, in hardwoods the wood thrush.

The forest of pure *Pinus* is characterized by its few birds. The oven-bird is the only conspicuous species beneath the canopy, while in the canopy the blackburnian warbler and black-capped chickadee are most noticeable. The pine warbler is diagnostic when present. *Tsuga* is characterized by its abundance of blackburnian and black-throated green warblers.

Depths of Territories

Certain species have different depths of territories in different forest types (Figs. 3-7). In the bog areas most of the activities of the yellowthroat are restricted to the 3-foot high shrub stratum and the ground, but frequently the males use stubs up to 20 ft high as song posts, or even have flight songs 20 ft above the ground. In *Picea mariana—Thuja,* however, where the shrub stratum is 10 ft high, this species remains entirely within that stratum. Thus the bird's niche has a certain minimum height above the ground—somewhere between 3 and 10 ft—which is governed by its song post requirement. The cedar waxwing usually ranges between the top of the shrubs and the top of the canopy, except where the canopy is sufficiently dense to restrict its frequent flights, as in *Picea mariana—Thuja.* Here this species remains beneath the canopy but above the dense shrub stratum. In bog where it can pitch down to the ground and up again between the hillocks of vegetation, and on the muddy river shores unimpeded by vegetation, its niche extends to the ground.

Some species, such as the olive-sided flycatcher, inhabit certain vegetational strata regardless of their height. This flycatcher inhabits the tree tops, which are 40 ft high on the edge of the bog (Fig. 3) and 70 ft high in *Picea mariana—Thuja* (Fig. 4). The white-throated sparrow nests on the ground in deciduous (*Betula—Populus*) as well as in coniferous forest, but shows an unwillingness to move upward into the tree foliage of deciduous forests.

The evidence suggests, then, that there are 2 major factors determining the depth of a territory and the height of a niche above the ground. One is the distance from the ground at which the bird prefers to live, and the other is the vegetational stratum or strata in which the bird finds its niche requirements fulfilled. Both of these factors are usually behavior responses, part of the mores of each species.

The Climax Forest

Kendeigh (1948) postulates that the birds of the coniferous forests of eastern North America fall into one community. Snyder (1950) notes that the birds of the climax coniferous forest in the Rocky Mountains of Colorado form a community that differs from the eastern coniferous bird community in species composition, zoogeographical origin (Old World and New World respectively), and migratory status (western species mostly limited to vertical rather than latitudinal seasonal movements).

According to the present analysis, there appears to be yet a third bird community of the coniferous forest, found in *Tsuga canadensis* forest and characterized by large populations of blackburnian and black-throated green warblers and a long list of other species.

According to Halliday and Brown (1943), *Picea glauca* and *P. mariana* survived part of the Pleistocene glaciation in a refugium in Alaska, while *Tsuga canadensis* and *Abies balsamea* passed this period in the Appalachian refugium. It seems feasible that the less hardy birds of the coniferous forest, such as warblers, could only have survived in the Appalachian refugium. At the present time in parts of this latter region, *Tsuga* forests are separated vertically from *Abies* by a zone of deciduous forest. Kendeigh (1946) found that in the Catskill Mountains of New York, the forest was *Tsuga-Fagus* at 750-2000 ft, *Fagus—Acer* at 1600-3500 ft, and *Abies—Picea* at 3200-4200 ft, with overlapping as indicated by these figures. Certain more boreal species showed a preference for the*Abies—Picea* forest, and most of the species here listed for the *Tsuga* forest occurred in the *Tsuga—Fagus.* If these 2 coniferous types of forest were also separated by hardwoods during the glacial period, different species could have become segregated into *Tsuga* forest at the lower elevation and into *Abies* forest at the higher elevation in the Appalachian refugium and possibly into the *Picea* forests of northwestern North America as well. According to Halliday and Brown, the *Picea* forests spread eastward to the Atlantic in an interglacial period, and spent the period of the Illinoian and Wisconsin glaciers in the Appalachians. Either at this time or in the subsequent northward spread of trees after the Pleistocene, the forests of *Picea* and *Abies* became intermingled as well as their bird life, while those of *Tsuga* remained distinct. This is apparently still reflected in the present day distribution of species.

SUMMARY AND CONCLUSIONS

In order to determine some of the possible relationships between forest succession and bird populations in Algonquin Provincial Park, Ontario, censuses of breeding birds were taken, using the spot-map method, in most of the major forest types during the breeding seasons of 1952 and 1953. The approximate areas of the bird territories were measured and the vertical depth of territories determined by recording heights above the ground at which birds were observed. From these data approximations of average territory volume were obtained for a number of species. Niche characteristics of birds were recorded, and notes were made on aspection.

In consecutive stages of the hydrosere, predominant species were the swamp sparrow and yellow-throat in bogs, white-throated sparrow and yellow-throat in *Picea mariana* forest, and white-throated sparrow and Nashville warbler in *P. mariana—Thuja* forest. In those plots having more diversified vegetation, and hence more niches, there were more bird species.

In consecutive stages of the xerosere, predominant species were the oven-bird and red-eyed vireo in pioneer deciduous forest, white-throated sparrow and magnolia warbler in *Abies—Picea* forest, oven-bird and black-capped chicakadee in immature *Pinus strobus* forest, red-eyed vireo and oven-bird in hardwoods, and blackburnian warbler and black-throated green warbler in *Tsuga* forest. There was some evidence of selection by birds primarily for deciduous or coniferous forest and secondarily for early or late stages of forest succession.

Plots of mixed forest border had larger populations of birds than forest interior plots, due to more species being present rather than to larger representations of each species.

Vertical dimensions of territories were small relative to horizontal dimensions, and consequently territory volume varied chiefly in proportion to area. Most birds nested near the bottoms of their territories, had songposts near the tops of territories and consumed insect larvae from the tree foliage or trunks.

The hiemal aspect lasted from about the first of December to the end of March. Seed-eating species were the most abundant birds during this period. The prevernal aspect extended throughout April and the vernal aspect throughout May. The aestival aspect lasted during June and July and the serotinal aspect during August. The autumnal aspect extended from about the first of September to the first of December. The heaviest bird migration was during May and September. Distinct bird communities were recognized in bog, boreal forest, *Tsuga* forest, and deciduous forest. These bird communities were differentiated into a distinct facies in each vegetation type.

Total bird populations per 100 acres were 286 territorial males of 13 species in bog, 232 territorial males of 32 species in boreal forest, 279 territorial males of 28 species in *Tsuga* forest, and 168 territorial males of 18 species in hardwood forest.

ACKNOWLEDGMENTS

Acknowledgments are made to Dr. S. C. Kendeigh who directed this study and critically read the manuscript of this paper, the Research Council of Ontario which provided financial support, the Ontario Department of Lands and Forests which provided most of the facilities, Mr. A. N. Martin who prepared the illustrations, Miss Constance Martin who granted financial assistance toward preparation of the manuscript, Acadia University which also helped finance the manuscript, Mrs. N. D. Martin who typed the early drafts, and many others who made major contributions to this investigation.

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SEASONAL POPULATION CHANGES AND HABITAT PREFERENCES IN THE GENUS *LACCOPHILUS* (COLEOPTERA: DYTISCIDAE)[1,2]

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Introduction

The aquatic beetles of the genus *Laccophilus* represent a specialized and highly successful group widely distributed over the earth. The genus is found in nearly every tropical or temperate region, and in some tropical areas as many as a dozen species may be found in the same or similar situations. Various workers have concluded on the basis of morphological characters of the adults and larvae that *Laccophilus* represents a relatively new and expanding group of beetles. If this is so, the species have not yet had time to complete the adaptation to diverse habitats, that is, to undergo the adaptive radiation seen in many aquatic groups. This diversification of habitat often lessens the effects of interspecific competition by separating various closely related forms.

Four species of *Laccophilus* are found in Indiana (Blatchley 1910). Three of these, *L. maculosus* Say, *L. fasciatus* Aubé, and *L. proximus* Say, are widely distributed over much of the eastern United States. They are more or less ubiquitous in habitat selection and occur, as adults at least, in almost any kind of aquatic situation. The fourth species, *L. undatus* Aubé, has been reported sporadically in Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, and Indiana. The 4 Indiana species frequently occur together in the same pond and often within a few inches of one another, persisting together over much of the year. The proximity of the species is even more remarkable in that they are aggressive predators which often betray cannibalistic tendencies and, if in aquaria, need to be kept under special conditions to hold down mortality (Hodgson 1953). The assumption is, therefore, that these species compete with one another to some extent and affect each other's existence.

Gause (1934) in presenting experimental support for the theoretical conclusions of Volterra (1931) and Lotka (1932) concludes that species competing for a limited supply of food can not persist together in the same microcosm. Thomas Park (1955) restates the concept in this way: "Using the Tribolium model we have again confirmed an assumption that species of relatively similar ecology, when living together as interspersed populations, create a situation inimical for survival of both." The complexity of natural situations prevent application of the types of models employed by these workers. Crombie (1947), also working with gramnivorous insects states, "Species occupying different ecological niches survived in the same medium: while of those occupying the same niche, one always was exterminated." The situation in *Laccophilus,* however, could be similar to that found by Lack (1945) in the cormorant and shag (*Phalacrocorax* sp.). He demonstrated that what was apparently a case of 2 morphologically very similar species (*P. carbo* and *P. aristotelis*) occupying the same niche and habitat was not the case at all. After close analysis it was shown that not only the food, but also the feeding areas and nesting sites, were different.

There is evidence that utilization of different prey is not the sole factor in permitting 2 species to persist in the same habitat. Lack (1946), from Uttendorfer's lists of prey species of German predatory birds, points out that, while no 2 congeneric species compete for the same food supply, there were 5 species of Falconiformes and 5 species of Strigiformes preying on a single species of often very abundant vole. Also, Crowell and Crowell (1946) reported the displacement of Common and Roseate terns (*Sterna hirundo* and *S. dougalli*) by Herring gulls (*Larus argentatus*) from the Weepecket Islands off Massachusetts. These workers thought that, although some predation (which is not competition) by gulls on terns was present, it was inability of the terns to reproduce successfully in the presence of the gulls that was of greatest consequence.

Andrewartha and Birch (1954, p. 404) state that competition is the ". . . relationship between species which utilize the same food and space." They also emphasize that competition exists only when food or space is limited in relation to the numbers of organisms utilizing it or when one species harms the other by fighting or in some other way. In this study competition is defined as the condition that exists when species of *Lac-*

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[1] Contribution No. 662 from the Zoological Laboratories of Indiana University.

[2] This work, part of a doctoral thesis, was done while I was a graduate student in the Zoology Department, Indiana University, under a National Science Foundation Fellowship for the academic year 1956-57.

cophilus are trying to capture the same prey species or to utilize the same habitat.

Little information is available about the prey of *Laccophilus,* but Wilson (1923) reared the larvae of 2 species and found that both accepted the same prey—larvae of *Chaoborus, Ceratopogon, Dixa, Peltodytes,* and *Hydroporus.* The behavior of the 2 was different, however, in that the larger species, *L. maculosus,* was much more aggressive—readily preying on its own kind and on the other species, *proximus.* The latter never indulged in cannibalism nor attacked *maculosus.* This worker has found from laboratory observations that the adults of the 4 Indiana species readily accept the same prey. Particular success was obtained with mayfly naiads, but it was necessary to injure the naiads first. Swarms of *Laccophilus* would cover the large naiads when this was done. Hodgson (1953) used hamburger for feeding *maculosus* kept in aquaria.

Elton (1951) defines niche as the activities of an animal particularly in regard to securing food and shelter. A convenient measure of niche, according to him, is the size of the animal and what it eats. The habitat, on the other hand, is the situation in which it is found.

In a given major habitat, the elaboration of many niches permits a large variety of organisms to be present with a complex food web, but to what extent the habitat can be "subdivided" is also involved in the problem of utilization of the environment by different species. The direct competition of related species should be minimized not only through diversification of niches, but also through the occupation of a minor habitat (*cf.* Young 1954). Restrictions of habitats presumably allows the coexistence in the same region of closely related species. Beauchamp and Ullyott (1932) showed that *Planaria montenegrina* and *P. gonocephala* could be found in the same streams, but at different altitude gradients. They determined, also, that *P. alpina* preferred flowing water, while *Polycelis cornuta* preferred pooled situations. Temporal as well as spatial occupancy of an area must be considered in determining the minor habitat of a species.

Modification of the environment by man also influences the relationships of species. Examples of population fluctuations of animals in disturbed areas are numerous. Examples in insects are not too well known, but Young (1950) records the decline and extinction of the Florida Blue butterfly (*Eumaeus atala florida*). Man had made inroads in the populations through disturbance of the habitat, but apparently not enough to result in the insect's complete disappearance. An immigrant arctiid moth from South America increased in abundance at about the time of the Florida Blue's decline. The moth caterpillar used the same food plant (a cycad, *Zamia intergrifolia*), and it voracious larva may have fed on the butterfly larvae or eggs as well. There are indications that at least one species of Indiana *Laccophilus* may be at a disadvantage in environments which have been disturbed by man.

The following study was undertaken to attempt to show (1) whether interspecific competition actually exists among the 4 Indiana species of *Laccophilus;* (2) to what extent this competition might affect their distribution, or the converse; and (3) some of the factors which may influence changes in the individual species populations.

Thanks are due to Dr. F. N. Young of Indiana University for his aid, helpful advice, and for putting at my disposal materials in the collection of the University of Michigan Museum of Zoology. Dr. D. G. Frey, Indiana University, was instrumental in making transportation available. Dr. Helmut Mueller and Dr. J. B. Stahl have identified plants for me. Also, Dr. J. L. Laffon, Iowa State College, Dr. D. D. Millspaugh, Iowa Wesleyan College, and H. C. Severin, South Dakota State Agricultural Station, lent museum materials for my use.

GEOGRAPHICAL RANGES

The limits of the ranges of Indiana *Laccophilus* are only vaguely known. The approximate ranges of the species are as follows:

Laccophilus maculosus Say is essentially a northern species (see map, Figure 1). The southernmost records are from the Appalachian foothills of northern Alabama and Georgia. Presumably, the southward extension of the range in this region is along the mountains. From the southern apex the limits follow a generally northwesternly diagonal to western South Dakota where *maculosus* overlaps the range of a very similar western species, *L. decipiens* LeConte (Zimmerman and Severin 1957). *L. maculosus* extends into southern Canada (Pettit 1869, Harrington 1884) and east to Mt. Desert Island, Maine, just off the Atlantic Coast (Proctor 1946). South of central Indiana the species seems to be found in progressively more restricted situations and less generally throughout the area.

Laccophilus fasciatus Aubé is especially common in open ponds and roadside ditches in the middle west (Figure 2). It ranges south to northern peninsular Florida but is rare except in the well-drained soils of the western part of the state (Young 1954). In eastern Texas it seems to

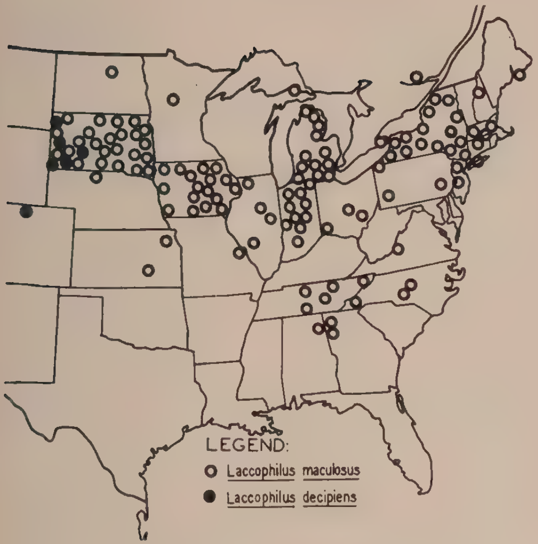

FIG. 1. Distribution of *Laccophilus maculosus.* Localities are based on published records, specimens in the University of Michigan Museum of Zoology, South Dakota State College Collection, Iowa State College Collection, and material in the writer's collection. The easternmost records of *Laccophilus decipiens* are included.

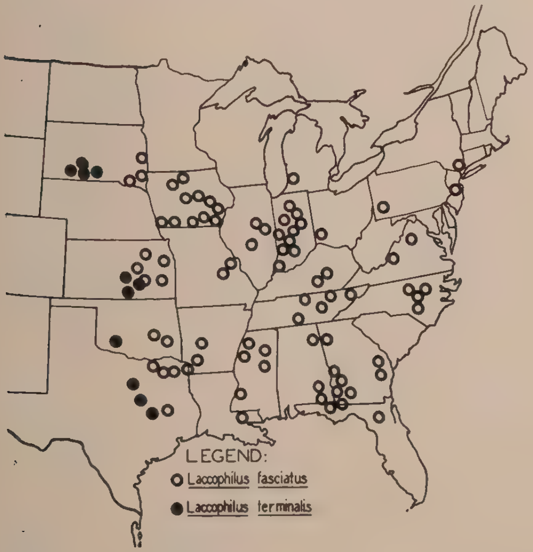

FIG. 2. Distribution of *Laccophilus fasciatus.* Localities are based on published records, specimens in the University of Michigan Museum of Zoology, South Dakota State College Collection, Iowa State College Collection, and material in the writer's collection. The easternmost records of *Laccophilus terminalis* are included.

be found no farther southwest than about the Brazos River. Here in the Cross Timbers region (Bowman 1911) it is occasionally encountered, but west of the Brazos *fasciatus* it is largely replaced by *L. terminalis* Sharp, a very similar, but distinct, species which extends west to southern California (Leech and Chandler 1956). The latter occurs to some extent east of the Brazos but there seems to be little overlap in the ranges of the 2. During this study there was no overlap found, but subsequent collecting by the author shows that in Sedgwick County in south central Kansas the 2 species do occur in the same situation. The western limits of *fasciatus* are not known in Oklahoma, Kansas, and Nebraska, but in South Dakota it apparently occurs only in the extreme southeastern part of the state (Zimmerman and Severin 1957). *L. fasciatus* extends eastward to the Atlantic seacoast reaching its northern limit in Iowa, Illinois, southern Michigan, Ohio, southern Pennsylvania (Hamilton 1895), New Jersey, and in the lower part of the Mohawk Valley, New York. The northern limit in the Appalachians is assumed to be more southernly than in nearby lowlands.

Laccophilus proximus Say extends over a larger area of the United States than the other *Laccophilus* found in Indiana (Figure 3). It seems, however, to be chiefly a southern species with a range extending (as part of a rasenkreis probably) into the Antilles and Central America (Young 1953, 1954). In the United States it is found from the extreme tips of southern Florida and Texas, as far west as the Davis Mountains, Texas, and north to northwestern South Dakota,

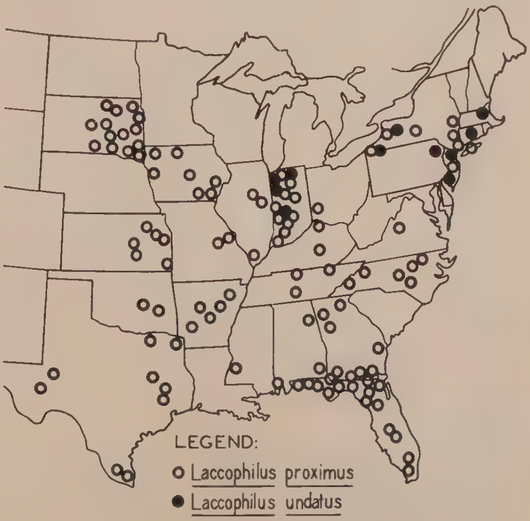

FIG. 3. Distribution of *Laccophilus proximus* and *L. undatus.* Localities are based on published records, specimens in the University of Michigan Museum of Zoology, South Dakota State College Collection, Iowa State College Collection, and material in the writer's collection.

southern Minnesota, Michigan, Canada, and southern New York.

Laccophilus undatus Aubé extends from Indiana to Massachusetts, but no records are available for much of the area between. The species apparently is confined to an area limited in north-south dimensions. Bloomington, Indiana, is the most southernly point from which it is presently known and a locality near Boston, Massachusetts, is the most northernly one. *L. undatus* seems to be characteristic of the shaded pools of the northeastern woodlands and Appalachian region.

SEASONAL CHANGES IN LOCAL POPULATIONS

In order to determine the relative sizes of adult populations and to correlate factors of the environment with changes in population size, collections were made at regular intervals in 1956 and part of 1957. Sampling was concentrated in 3 types of small aquatic situations in the vicinity of Bloomington, Indiana.

Sampling Methods

Nearly all collections were made with small kitchen strainers (6 inch diameter wire sieves). The small strainer produces little alteration of natural conditions. Large aquatic insect nets were used on only a few occasions because it was feared that continuous use of such nets would destroy much of the marginal vegetation in which *Laccophilus* are usually found and also that mass collections might influence later fluctuations in the populations. Even the small strainers may have affected the later counts to some extent, but the effect is thought to have been minimal.

An effort was made to standardize the individual collections by visiting the same specified small area each week, and (1) collecting intensively in the distance of an arm's length, and then, after 3 or 4 sweeps of the net which fail to produce any *Laccophilus,* moving to another spot, and (2) collecting intensively for a specific length of time—15 or 30 minutes depending upon the size of the situation.

The usual procedure when taking samples was as follows: After temperature and changes in water level were recorded, a few exploratory sweeps of the strainer were made to locate concentrations of individuals—*Laccophilus* can usually be found in clumps. Any emergent and submergent vegetation in water of not more than a foot in depth usually proved most productive and was investigated first. In Pond 4, which was in an abandoned quarry, stirring algal mats often revealed large numbers of *maculosus* but in other situations this was not found to be true. The insects usually remain attached to leaves, debris, or other objects in the water, but observation for several minutes often revealed the beetles surfacing to renew their air supply. Scraping the bottom with the strainer turned sideways to sweep in any beetles just below the surface of the bottom debris proved profitable. Pushing the strainer with the opening up into bunches of sedges also trapped many beetles which swam downward into it. Upon netting, the specimens were transferred by pipette (with the tapered end cut off) to 80% alcohol and identified in the laboratory.

Specimens were listed by locality, were scored as to condition, whether teneral (callow) or not, and were identified to species. The results of the collections are sumarized on Figures 4-8 and in Tables I and II. The data for Ponds 1, 2, and 3 are plotted semilogarithmically. Pond 1 (Fig. 4) shows only half of the individuals per sample since sampling time was twice that at the other ponds.

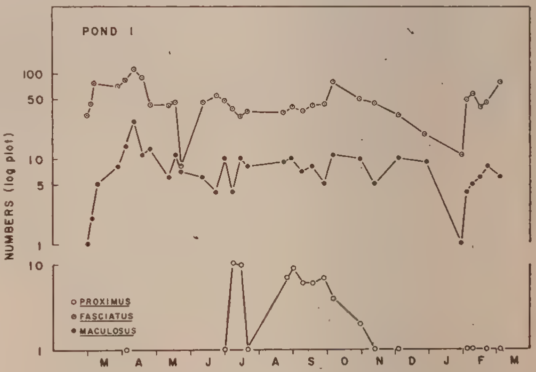

FIG. 4. Graph of the relative numbers of the species of *Laccophilus* in Pond 1 from samples taken from March 1, 1956 to March 4, 1957.

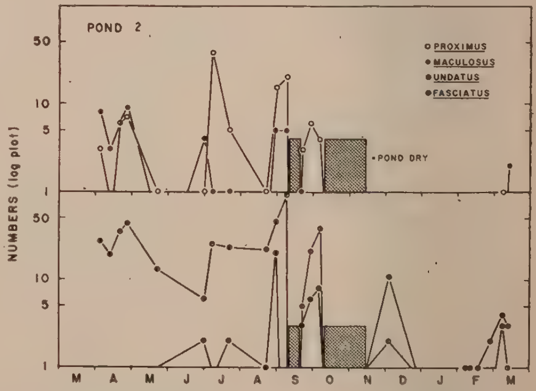

FIG. 5. Graph of the relative numbers of the species of *Laccophilus* in Pond 2 from samples taken from April 4, 1956 to March 13, 1957.

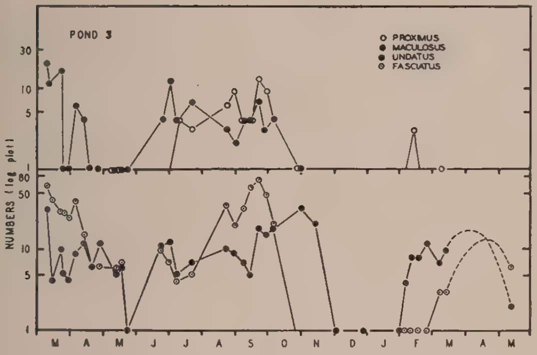

FIG. 6. Graph of the relative numbers of the species of *Laccophilus* in Pond 3 from samples taken from March 6, 1956 to April 13, 1957.

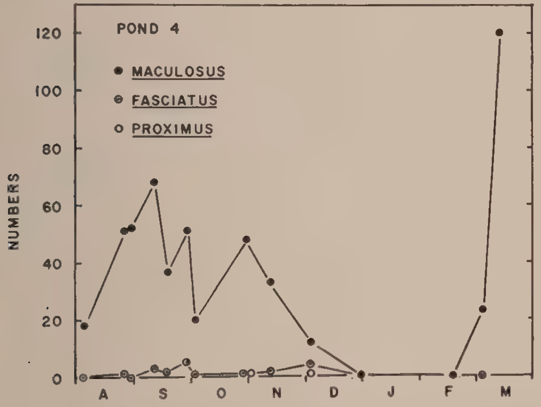

FIG. 7. Graph of the relative numbers of the species of *Laccophilus* in Pond 4 from samples taken from August 5, 1956 to March 13, 1957.

TABLE I. *Laccophilus* taken from four small aquatic situations in the vicinity of Bloomington, Monroe County, Indiana

Pond	number of collections	SPECIES fasciatus No.	%	maculosus No.	%	proximus No.	%	undatus No.	%
1.......	33	3434	82.7	561	13.4	183	3.9	..	..
2.......	23	428	65.3	45	6.9	119	18.2	63	9.6
3.......	30	930	55.6	166	9.9	113	6 7	468	27.9
4.......	13	21	3.8	530	95.8	2	0.4	..	..
Totals..	99	3933	63.6	1302	21.1	417	6.7	531	8 6

Descripiton of Habitats

The ponds of this study lie in the unglaciated limestone of the Mitchell Plain district of southern Indiana. Not any of the situations are "natural" in their present state, since they were constructed or resulted by some type of human disturbance. Ponds 1, 2, and 3 are within the alluvial "flats" bordering Bean Blossom Creek in areas of either Waverly or Holly silt loam soils.

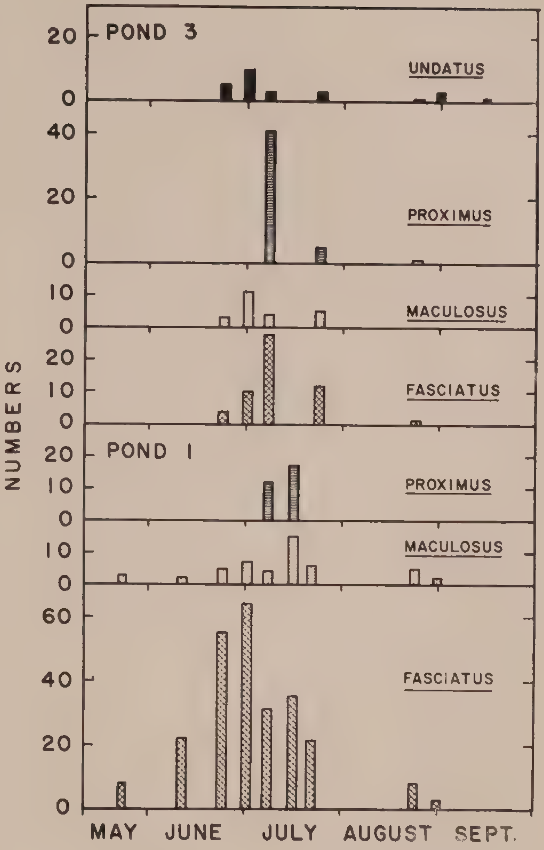

FIG. 8. Bar graph of *Laccophilus* tenerals (recently emerged adults) collected from Ponds 1, 2, and 3 from May through September, 1956. The totals for ponds in the slough (2 and 3) are lumped as Pond 3.

TABLE II. Results of sampling to test possible segregation of species of *Laccophilus* contemporarily occupying the same aquatic situation

	POND 2		POND 3				POND 1			
Date.......	8/30/56		8/30/56		9/21/56		10/30/56		11/22/56	
Species	edge	mid	edge	mid	edge	mid	edge	mid	edge	mid
undatus.........	2	26	2	8	2	16	..	..	..	..
proximus.......	17	8	9	0	18	3	3	1	..	1
fasciatus........	40	4	20	2	60	45	71	85	54	48
maculosus.......	1	4	1	1	4	7	24	11	4	3

Pond 1

An artificial pond in an open pasture, referred to hereafter as Pond 1 has a circumference of approximately 60 meters and is about a meter deep which corresponds to a small pond in Pichler's classification (1939). The soft mud bottom seems little differentiated from the soil in which it is located, although there are probably chemical differences due to submergence. The pH of a water sample taken on March 22, 1957 at 2:30 p.m. was 8.2. A small amount of leaf debris and a filamentous algae, *Pithophora,* are the most prominent bottom features that provide concealment and attachment for the beetles.

The water surface averages about three-quarters of a meter below ground level. Little change in depth is apparent in the months from December to May. From May until late November the depth gradually decreases, but during the study the decrease was not more than about 30 centimeters. About 60% of the shoreline slopes gradually into the water and the remaining 40% more closely approximates a right angle. The steeper banks are largely stabilized by grasses which are typically absent on the more gentle slopes. It is in the water along the steeper banks that the *Laccophilus* seem to be concentrated.

The little emergent vegetation of this turbid pond is mostly tufts of *Eleocharis* and *Sagittaria.* The pasture grass which grows up to the edge and frequently falls over into the pond is the predominant marginal vegetation and provides habitats for *Laccophilus.*

No fish were seen until the second spring of observation. The pond was teeming with fry after that time. In this pond vertebrate predation can be considered neglible. The pond supports an extensive invertebrate and insect fauna other than the Coleoptera. The presence of the phantom midge, *Chaoborus americanus,* and predatory midge, *Procladius* sp. was noted.

Ponds 2 and 3

Several small ponds occur in a slough in the drainage of a former intermittent stream about 1 mile from Pond 1. Two have been designated as Pond 2 and 3. These two ponds were acidic (pH 6.6) in contrast to most other water bodies in this area. The ponds are part of a low-lying area which, within a radius of 500 meters, is waterlogged from December until April.

Pond 2 has two basins which are separated by a 20-25 cm sill. One basin is about 45 cm deep and the other is about 35 cm deep at maximum making the station a pool by Pichler's classification (Young and Zimmerman 1956). By the end of May, however, the pool seldom exceeds 20 cm which puts it in the puddle category, and by mid-September both basins may be dry. The pool measures about 9 by 28 meters. Widely scattered emergent plants afford the only shade.

Pond 3 has irregular and indefinite margins and in the spring covers more than 100 square meters, but is seldom deeper than 90 cm. A grove of trees on the south bank furnishes more shade than in either Pond 1 or 2. During the colder months Pond 3 receives direct sunlight for only 4 or 5 hours per day and for this reason has consistently lower surface temperatures than many other ponds in the vicinity.

Scirpus is abundant along the margins and is the principal emergent plant. About half of the bottom of the ponds is covered with *Ludwigia palustris* and *Zannichellia.* The *Scirpus* and *Ludwigia* plants form extensive mats which were generally absent in Ponds 1 and 4. Early in the year *Scirpus* is the principal component, especially at the margins, but by August the water's edge has receded to the thick beds of *Ludwigia.* In spring and early summer filamentous algae fills both ponds. Figure 9 is a composite diagrammatic profile of Ponds 2 and 3. A considerable amount of organic material (leaves, dead aquatic plants, and cattle manure) is deposited into these ponds.

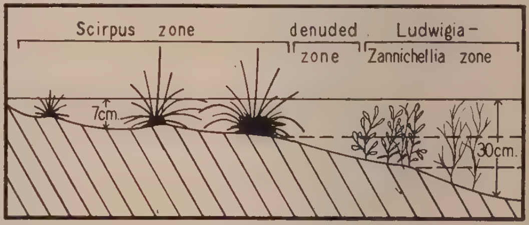

FIG. 9. Composite diagrammatic profile of Ponds 2 and 3 showing approximate zones of vegetation. Dotted lines show water levels in August (the upper) and November (the lower). The denuded zone is the marginal area during the concentrations in the fall. *Laccophilus undatus* was commonly found in the *Ludwigia-Zannichellia* zone and the other *Laccophilus* were more commonly in the *Scirpus* zone.

Ponds 2 and 3 exhibit different variations in respect to their surface temperatures following warming periods. Pond 3 never exceeded 30° C on any observation, while 2 had temperatures of more than 30° C on 3 occasions. Similarly, after a rapid cooling occurred, Pond 2 underwent the more rapid drop in temperatures. At a depth of 20 cm Pond 3 also lagged behind 2 in the spring warm-up.

In Pond 3 fish predation, particularly by the green sunfish, *Lepomis cyanellus,* could not be entirely disregarded. These small fish were taken in the strainer in shallow water (5 cm and under) which most *Laccophilus* prefer.

Pond 4

Quarry operations immediately north of Bloomington have produced an area in which numerous shallow pools have developed and some of the pools have been in existence long enough for water plants such as *Typha* and *Cyperus* to be present.

The largest pool, hereafter referred to as Pond 4, is approximately 50 meters wide and 150 meters long. Water depth reaches about 1.5 meters in one small basin. This basin lies about 3 meters from the west margin of the pool, but slopes gradually upward in the other directions. The face of quarry wall rises almost perpendicularly to a height of about 60 meters at a distance of about 4 meters from the west edge. It is along this margin that most *Laccophilus* are found. On sunny days this part of the pool is heavily shaded every afternoon. *Laccophilus* is rare in this pool except at the margins in water less than 30 cm deep, but in this zone it is the commonest water beetle.

The bottom of Pond 4 is in part bedrock and in part limestone chips and dust. Some of the surrounding red clay soil has washed into the water as well. The pH in March was about 7.6.

During the period of observation the water in Pond 4 remained exceptionally transparent, but from August (when sampling began) until November an algal scum covered the bottom and floated in extensive mats at the surface. Both rainwater and seepage water enters the pool accounting for the fact that it never was dry in spite of the wide area and general shallowness. The margins of all but the west side varied greatly from month to month, but, since the slope was much steeper on the west, a fluctuation in water level produces little change in the area covered. Pond 4 is an atypical habitat except for Monroe and adjacent counties.

Results of Sampling

The ponds and pools of this study differ in physical characteristics, amount and kind of vegetation, shape and permanency of the water body, nature of the substrate, and the rates of temperature change. Since the species of *Laccophilus* are probably not affected to the same degree by the environment, the variation in habitats should affect changes in different species to a different degree. If it is possible to correlate physical differences with population changes or with the abundance of one or more of the species it should be possible to analyze some of the influences affecting the distribution of *Laccophilus*.

Considerable variation in numbers was observed in every species. Some of the variations can be attributed to weather and sampling error, but some of the variations must result from biological properties.

Laccophilus fasciatus

Laccophilus fasciatus was present more frequently and in greater numbers than any of the other 3 species (Table I). In Pond 1 it formed an overwhelming preponderance of the total *Laccophilus* (over 80%), and in a total of 33 collections never less than 15 *fasciatus* were captured on any visit.

The changes in the numbers of *fasciatus* in an annual cycle can be grouped into 4 different phases (Fig. 4). Two maxima and 2 minima are evident.

Beginning sometime in February, depending upon weather conditions, the number increases very rapidly to a maximum in early April. This increase is due to the reappearance of overwintering individuals. A very small percentage (less than one %) is due to the emergence of teneral adults (very recently emerged individuals in which the exoskeletons have not fully hardened).

The second phase is a decline in which the population drops to its lowest level from April through late May. This decline probably reflects the mortality of overwintering individuals. Near the end of May only 15 *fasciatus* were recorded, which contrasts sharply with 226 taken one month before. Toward the end of May, however, the number and percentage of tenerals increases.

In June the number rises again but does not reach the previous level. This intermediate level is maintained, or rises gradually through late August. The maximum occurs near the end of June in Pond 1 but it may be later at the other stations (Figs. 5, 6). The rise appears to be entirely due to emergences. A gradual increase continues to a new high in early October. The autumnal level may be higher or lower than the peak observed in the spring. In Pond 1 the number was not so great, but in Ponds 2 and 3 the totals were higher than at any other time. The sample size in this period would depend in large part on the comparative reductions in pond area. Ponds 2 and 3 had shrunk to no more than one-fifth of their former area while Pond 1 was relatively unchanged. Increase in numbers reflects concentration as well as additions to the population. In support of this it is noted that the number of tenerals taken in September and October was low.

Coinciding with the onset of freezing temperatures, the population enters the fourth phase in which *fasciatus* decreases either constantly as in Ponds 1 and 4 (Figs. 4, 7), or suddenly as in Ponds 2 and 3 (Figs. 5, 6).

In Pond 4 (Fig. 8) the number of *fasciatus* remained too low to indicate phases. The chief generalization is that environmental conditions there were not favorable for support of a large *fasciatus* population. The presence of a large *maculosus* population indicates that perhaps the former species could not establish large numbers because of pressure from the latter as well as unfavorable physical conditions.

Laccophilus maculosus

This species was found consistently in Ponds 1 and 4 (Figs. 4, 7). It was the most frequent and numerous beetle collected in Pond 4, but persisted in lower numbers than *fasciatus* in Pond 1. An early spring maximum occurred in all stations (In Pond 4 only the emergence period of June and July is not included in the sampling). The decline in late spring was clearly discernible for *maculosus* in Ponds 2, 3, and 4. For a period of nearly 2 months *maculosus* was almost absent from these stations and never more than a single *maculosus* per sample was taken from Pond 2 from mid-April until the end of June.

Little change is evident following the rise in numbers in July in Pond 1, although tenerals appeared in June, July, and August. Samples during that period included a mean of about 8 *maculosus* individuals. The decline in autumn varied considerably in the time of its onset. In Ponds 2 and 3 decline appears in early October, in Pond 4 near the end of October, but in Pond 1 not until December 31.

Laccophilus proximus

L. proximus appeared sporadically in all 4 ponds, and was not taken at all during several months of the year. The total number of *proximus* was less than that of the other three species (Table I).

A spring maximum was seen in only one station—Pond 2 (Fig. 5), and even there none was taken in one of the samples during that period. No general increase could be shown until July, but at that time sharp increases occurred at all stations, attributable to the emergence of tenerals. In Pond 2 the number of individuals increased from one to 37 (all teneral) in one week.

After emergence, a decrease seems to occur in *proximus* populations. Two weeks after emergence in July in Pond 2 the number had dropped to 5, and in Pond 1 from 10 to one. One possible explanation for the decreases following emergences may be emigration from the pond. Laboratory observations indicate that under crowded conditions (50 to 100 individuals in a half-filled bowl of 4 inch diameter) *proximus* readily left the water and flew away, while the other *Laccophilus* seldom did. Young (1954) describes *proximus* as a pioneer species of new situations in Florida and characteristic of temporary ones. Since some ponds are probably more suitable for larvae than adults, it seems plausible that, through crowding pressure and other factors, *proximus* tends to spread quickly to less favorable ponds, as do other dytiscids (Balfour-Browne 1950).

This species also showed the effects of the reduction of available habitats in the late summer and fall as seen in the increased size of the samples take in Ponds 2 and 3 (Figs. 5, 6). In Pond 2 *proximus* readily reestablished a population after the first dry period in September, but was apparently unable to do so following the second dry period. No *proximus* could be found later than the first week in December.

It is interesting that 3 *proximus* were taken in Pond 3 (Fig. 6) as early as February 14. Two or 3 warm, sunny days preceded the date on which this sample was taken. The very shallow margins of this pond are subject to rapid warming. Temperatures of 20° C were recorded in the marginal area (7 cm *Scirpus* zone of Figure 9) on March 28, while at 20 cm depth the temperature was only 14° C. This species appears to be more sensitive to temperature changes than the other 3.

Laccophilus undatus

This species had not been reported for southern Indiana before the beginning of this study. Blatchley (1910) lists the species from only 2 counties in northern Indiana, and Young (personal communication) had taken it in only one county, Tippecanoe, in the central part. It has been found in only 2 locations in Monroe County to date, and these are within a few hundred meters of one another. In 2 of the stations, Ponds 2 and 3, *undatus* commonly occurred throughout the year, however.

L. undatus shows a pattern similar to *fasciatus* and *maculosus* but with important modifications. The spring increase begins very early in February, and by early March its numbers have reached a high level (Fig. 6) but, as in the other species, a drop takes place in April and May. Coinciding with the emergence of tenerals (Fig. 8), a population build-up begins in June and reaches a peak in late autumn (Fig. 6). A maximum occurs in late October which is a later period than that found for the other species at the same station. *L. undatus,* unlike *proximus* and *fasciatus,* reappeared in Pond 2 quickly and in appreciable numbers after it refilled in November (Fig. 5). In Pond 3 (Fig. 6) *undatus* is the predominant *Laccophilus* during the colder half of the year.

Comparison of the Populations

Table I summarizes the total of each *Laccophilus* species for each of the 4 stations. The number of *fasciatus* clearly exceeds the others, forming over 60% of the total. In spite of this general numerical preponderance of *fasciatus,* the percentage of *maculosus* (95.8) in Pond 4 represents the largest fraction of any species for a single station. This heavy numerical advantage was maintained throughout the period of observation (Fig. 7) which indicates that it was not merely a seasonal phenomenon. Also, regardless of the overall preponderance in numbers of *fasciatus,* several samples contained more of one or another of the species. *L. maculosus,* as cited above, was the most striking case; but in Ponds 2 and 3 (Figs. 5, 6) during the months from October through February, *undatus* was the most abundant species, and, finally, *proximus* formed the largest percentage of the 4 species on July 7 in Pond 2.

Two samples from successive years in Pond 1 agree closely. The sample of March 9, 1956, includes 154 *fasciatus,* 10 *maculosus,* and no *proximus,* which compares favorably with 158 *fasciatus,* 11 *maculosus,* and 1 *proximus* collected on March 4, 1957. The agreement of these samples lends support to the standardization of the technique used. Moreover, trends were repeated. In both years the phases of *maculosus* lagged behind those of *fasciatus* (Fig. 4) by about 2 weeks. Large increases for *fasciatus* appeared in February and early March, but the largest increase for *maculosus* was not until April. The peak for both, however, occurred on the same day.

L. fasciatus seemed to be more numerous near then north bank in Pond 1. The north bank receives more sunlight than the south one and, if overwintering takes place along these banks, the individuals overwintering there would be warmed earlier.

Some delay in the increase of *maculosus* was also evident in Ponds 2 and 3. Conversely, the decline in the late spring seems to take place later for *maculosus* than for *fasciatus* (Fig. 4). The ebb point in this drop for *fasciatus* was apparently around May 22, but for *maculosus* it was not until about June 23. The same delay was found in Pond 2.

The greatest number of emergences of all species took place from May through August, although some tenerals were found in all seasons. In Pond 1 the largest numbers of teneral specimens of *fasciatus* were found near the end of June and the first of July. This suggests that the time of emergence is later for *maculosus.* In Ponds 2 and 3 (Fig. 8) the situation appears reversed, but this is probably due to sampling error. The general correlation of the northern *maculosus* with more permanent aquatic habitats and an apparent preference for shaded situations are also possible reflections of the adaptation to a colder climate.

Prominent fall peaks were observed in all species except *maculosus.* The peak of *proximus,* the most southern species (Fig. 3), appeared in early September (Fig. 5), the peak for *fasciatus* in late September (Figs. 4, 6), and that for *undatus* in October (Fig. 6). Each species appears to have a different chronology which seems to bear a relationship to geographical distribution

In autumn, when the populations were relatively concentrated, segregation of *fasciatus, proximus,* and *undatus* into separate parts of the habitats seemed to be present. In order to test this, samples were taken on August 30 and September 21 in Ponds 2 and 3, (1) along the extreme margin in water less than 3 cm deep (corresponding to the denuded zone of Figure 9), and (2) in the deeper central part of the ponds where the water was up to 30 cm deep (*Ludwigia-Zannichellia* zone of Figure 9). At this time the approximate dimensions of the pond were reduced to less than a tenth of their former maximum extent.

Sampling in Pond 1 was similarly divided: (1) in water less than 20 cm deep, or in the marginal area, and (2) in water over 20 cm deep, or in the central area. The extent of this pond had decreased little from its maximum area, but it had decreased about 30 cm in depth. The samples were taken on October 10 and November 11. Table II summarizes the results in the 3 stations.

The differences in frequencies found for *undatus, proximus,* and *fasciatus* are statistically significant at the one % level by the Chi-square test, but are not significant in Pond 1. The data for *maculosus* showed no statistical significance, although they were slightly above the 5% level in Pond 1. *L. fasciatus* and *proximus* remain in a very narrow band along the extreme margin of the remnant puddle while *undatus* is largely confined to the middle.

One possible explanation of segregation may be preference for a higher or lower temperature. The recorded temperatures of the water in Ponds 2 and 3 for these periods were as follows:

August 30, Pond 2: surface 24° C, 20 cm 22° C.
August 30, Pond 3: surface 27°C, 20 cm 22°C.
Sept. 21, Pond 3: surface 21° C, 20 cm 17° C.

Differences in the temperatures at the surface and at 20 cm were evident even in these shallow pools. *L. proximus* and *fasciatus* seemed to prefer warmer water, while *undatus* was restricted to the cooler water. Another explanation may lie in the amount of vegetation that was present in the middle part of the pond, but which was absent in the margins. Throughout the study *undatus* was regularly associated with some vegetation in the water.

Possibly segregation was not clearly shown in Pond 1 because of the later testing period; or another factor could have been less reduction of available area in Pond 1 than in Ponds 2 and 3. Also, the subdivisions used for the sampling areas may not have been distinct enough to obtain any significance. For example, a separation above and below 20 cm may have included too much of the area of overlap of *maculosus* and *fasciatus*.

Some evidence for the displacement of *undatus* by the other 3 species (or probably only by *fasciatus*) through competition was seen during the first part of September. All 4 species were present in Pond 2 on August 30 (Fig. 5), but on September 8, no *undatus* were taken while the others were even more numerous. More *fasciatus* were collected on that date from Pond 2 than at any other time. The temperature of the water must have affected the behavior of *undatus*, but it cannot be assumed that temperature alone caused the disappearance. *L. undatus* was still present in Pond 3 (where concentration was not so extreme) along with large numbers of the other *Laccophilus*. Under what were probably less extreme conditions, *undatus* was able to persist with the other species. Since the numbers of *undatus* were increasing in Pond 3 (Fig. 6), it is assumed that they migrated to it from less favorable spots, such as Pond 2. Minor habitat segregation cannot be expected to minimize competition enough to allow the persistence of less well-adapted species in periods of extremely high concentration. About a month later when Pond 2 was again reduced to a level comparable to that of the preceding month, *undatus* had reappeared and persisted despite lower temperatures.

L. maculosus was not found in Pond 2 in October, thus emphasizing the avoidance of temporary situations by that species. Lower temperatures could not be considered as the controlling factor since *maculosus* could still be found in all other stations and, also, because *maculosus* has a geographical range which extends farther north than the other species.

Discussion

The same pattern of population fluctuations is apparent for the adults of each of 4 species of *Laccophilus* occurring in the vicinity of Bloomington, Monroe County, Indiana. The pattern may be divided into 4 phases as follows:

(1) An early spring period of abundance due to the renewed activity of overwintering individuals of the previous winter.

(2) A late spring decline due to the mortality of the insects from the preceding year.

(3) An early summer period of abundance due to the emerging individuals of a new generation. This peak levels off or gradually increases until about September resulting in a higher peak in autumn due to (a) continuing emergences and (b) population concentrations resulting from the reduction of suitable habitats by evaporation. This peak is probably in part more apparent than real.

(4) A cold weather decline due to an increasing number of individuals becoming inactive (overwintering).

The second and third phases appear to result from intrinsic factors rather than from environmental changes. Temperatures, water levels, and vegetation are undergoing gradual modifications while *Laccophilus* appears to be rapidly increasing or decreasing.

The fluctuations are in contrast to the results presented by Omer-Cooper and Tottenham (1932) in which they found little change in the sizes of dytiscid populations in Wicken Fen, England. As far as can be determined, their collections were made at only 3 different periods—in March, July, and August. If collections were made at only these times in Indiana, it would also seem that the populations are fairly constant. Large changes, however, occur in April, June, September, and October. The influences of climate could, of course, account for a different picture than that in southern Indiana.

No one species seem to be equally successful in all sitautions. *L. fasciatus* shows a preponderance in unshaded ponds and the margins of small streams, while *maculosus* prefers more permanent situations which are frequently heavily shaded. The nature of the soil or soil-forming material adjacent to a pond also influences the success of a species by limiting the area suitable for pupation. Young (1954) states that in Florida *fasciatus* is commonest in muddy or silt-bottomed temporary pools occupying roadside ditches or intermittent streams traversing well-drained soils. The same habitats occur frequently in southern Indiana where *fasciatus* is the commonest *Laccophilus*. In Pond 4, where *maculosus* is the most abundant, however, the bottom and margins are mostly limestone chips and dust and are quite different from the well-packed clay soils which are more typical in Monroe County. Additional evidence is provided by a series of collections made by the writer in northern Indiana. An abrupt decrease in the number of *maculosus* compared to *fasciatus* was shown on October 26, 1956, in a north-to-south transect from near Wolflake, Indiana, southward. The collections extended across the southern boundary of the Steuben morainal lake area (Wayne 1956) into the Tipton till plain. Just north of the boundary 29 *maculosus* only were taken in a sample, but just 12 miles to the south a sample contained 3 *maculosus*, 35 *fasciatus*, and 1 *proximus*. The effect of climate could be discounted in such a short distance. The collections were from roadside ditches in which the most prominent physical difference noted was the change from the porous glacial Wisconsin Outwash soils of the Indiana lake region to the Tipton Till clay soils of central Indiana.

L. proximus is less abundant than *maculosus* or *fasciatus* in southern Indiana in most situations, but it is most commonly found in shallow, temporary pools exposed to the sun. In Pond 2, which had two basins, several *proximus* larvae, but neither adults nor larvae of any other species were found. These larvae were taken in the shallower basin that had previously dried at a time when the deeper one had not. The former had partially refilled after a short rain in September, but only for a brief period before both basins became completely dry. Adults of all 4 species were present in the deeper basin but no larvae could be found. *L. proximus* may need considerably less time to pass through the various larval stages than the other species, and, if so, this would give the species a distinct advantage in utilizing temporary situations.

L. undatus is restricted in Monroe County to a few shaded, marshy situations which have abundant emergent and submergent vegetation. A slightly acid condition existed at least part of the time in the slough where this species was always found. The temperatures probably remain lower than in most of the ponds in the vicinity.

Summary and Conclusions

A study of the seasonal population changes and habitat preferences of the 4 Indiana species of the genus *Laccophilus*—*L. maculosus*, *L. fasciatus*, *L. proximus*, and *L. undatus*—in Monroe County, Indiana, was made to determine if interspecific competition was present, and if so, to what degree. Attention was focused on seasonal changes and habitat differences since there seems to be little difference in the niches of the 4 species. The geographical distribution of these species is presented in so far as is possible from literature, museum collections, and personal collecting.

Collections were made at regular intervals over a period of about 14 months in 4 small aquatic situations, chosen for their large and persistent populations and for their contrasting physical characteristics.

Large fluctuations, divided into 4 phases of 2 maxima and 2 minima, were found in the populations of all 4 species. One maximum and minimum appeared due to the inherent biology of the insects, but the other two changes could be correlated with climatic and physical changes in the environment. The pattern of the phases varies in each species both in time and size of the fluctuations. Using the populations of *L. fasciatus* as a model (this species seems best adapted to this area as shown by its larger numbers and its greater frequency), it is seen that the populations of *L. maculosus* lag behind in phase timing. Although apparently at a disadvantage in warm weather, *L. undatus* predominates over all other species during the colder months in the ponds where it occurs. *L. proximus* is more mobile, and is more sensitive to temperature changes than the other species. Physical factors which seem to have an effect on the abundance of species are temperature, amount of vegetation, shading of the water surface, shore margin profiles, and the nature of the soils or soil-forming materials adjacent to the water.

There is some indirect evidence for interspecific competition among *Laccophilus*, but if competition does exist it is present for only 4 or 5 days in the year. Habitat selections and seasonal distribution tend to minimize the interaction among species. During periods of high concentration in the late summer and fall, segregation into restricted portions of the habitat is indicated for *L. proximus*, *L. fasciatus*, and *L. undatus*, but not for *L. maculosus*. *L. fasciatus* and *L. proximus* are restricted to marginal areas in 2 ponds while *L. undatus* occupies the deeper middle portions. In Pond 4, where *maculosus* was so abundant in the margins, *fasciatus* and *proximus* were found in very small numbers (less than 4 and one % respectively of the total taken).

The geographical distribution reflects the minor habitat of each species.

L. undatus represents a group different from the other 3 Indiana species on the basis of morphology, habitat, and geographical distribution. *L. undatus* appears to be a relict species of the eastern deciduous forest of North America and is at a disadvantage in southern Indiana under present conditions. Apparently, it is unable to exploit the many small aquatic situations resulting from human disturbance, and it seems to lack whatever preadaptive traits are necessary to make possible the extensive exploitation seen in the other species. *L. maculosus, L. fasciatus,* and *L. proximus* extend over wide areas of eastern North America, while *L. undatus* has only been found in a limited north-to-south zone from the northeastern to the midwestern United States.

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SOME EFFECTS OF TEMPERATURE AND COMPETITION ON THE DISTRIBUTION AND RELATIVE ABUNDANCE OF *APHYTIS LINGNANENSIS* AND *A. CHRYSOMPHALI* (HYMENOPTERA: APHELINIDAE)[1]

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Introduction

For the past 10 years 2 insect parasites, *Aphytis lingnanensis* Compere and *A. chrysomphali* (Mercet), have existed in southern California in nearly identical ecological niches. These 2 species are closely related ectoparasites of the California red scale, *Aonidiella aurantii* (Mask.), one of the most troublesome citrus tree pests. This scale species constitutes the only suitable host available to either parasite in the areas of this study.

Both parasites attack the same stages of the host and have very similar life histories and habits. Individuals of the 2 parasite species live in the same manner, in the same type of environment, and on identical food, both as larvae and as adults. At low magnification they are readily distinguishable only in the pupal stage; at higher magnification adults can be distinguished by an expert.

Aphytis chrysomphali has been present in California for about 60 years, presumably having been accidentally introduced, directly or indirectly, from the Mediterranean area. It became generally distributed as a parasite of the California red scale in southern California many years ago, but was much more common in some areas than in others.

Aphytis lingnanensis, a purposeful introduction from the Orient, was colonized throughout southern California by the Department of Biological Control, Citrus Experiment Station, Riverside, beginning in 1948 in an effort to obtain better biological control of the California red scale. From that time to the present these species have been in direct competition wherever they coexist.

After colonizing *Aphytis lingnanensis* in 21 field plots in which *A. chrysomphali* already existed, it was found that *lingnanensis* usually became dominant, sometimes to the point of apparent extermination of *chrysomphali,* in a period of from 1 to 4 years (approximately 10 to 40 parasite generations) (DeBach 1954). To quote from the same paper:

> This is somewhat surprising for two reasons: (1) "A" [= *lingnanensis*] has nearly completely replaced *chrysomphali* in certain plots in which extremely low host-scale densities were being maintained originally by *chrysomphali,* and (2) "A" [= *lingnanensis*] and *chrysomphali* adults are so similar that taxonomists have generally considered them to be the same species. One major difference is the general presence of males in "A" [= *lingnanensis*] and the general absence of males in *chrysomphali* in the field. What then could be the obscure differences that favor *Aphytis* "A" [= *lingnanensis*]?

Various laboratory studies then were conducted on comparative longevities, reproductive capacities, and rates of development at different temperatures, and it was stated that:

> Consideration of all the preceding data leads to the conclusion that *Aphytis* "A" [= *lingnanensis*] in most cases possesses superior intrinsic biological and physiological capabilities in comparison with *chrysomphali.* These results appear to explain in part at least why *Aphytis* "A" [= *lingnanensis*] has been so successful in competition with *chrysomphali* in the field.

We were quite satisfied with this work, which was rather intensive and had involved the assistance of several well-trained technicians, all of whom in 1951 shared the conclusions outlined above. It seemed just a matter of time until *lingnanensis* should disperse throughout southern California and virtually, if not completely, replace *chrysomphali.* Then, as so often happens in biological research, our conclusions suddenly appeared to be contradicted.

Following large monthly test colonizations of *lingnanensis* in a new plot in an untreated coastal lemon grove at Goleta, near Santa Barbara, from September, 1951, until November, 1954, it was found that *lingnanensis* never became dominant over the already established *chrysomphali.* Each species continued to exist in more or less equal numbers for 3 years in spite of continued colonizations of *lingnanensis.* Always before in other plots, colonizations of *lingnanensis,* especially on such a large scale and for so long a period, had greatly reduced *chrysomphali* populations in relation to those of *lingnanensis.*

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No colonizations were made in the Goleta plot after 1954, and in 1955 *chrysomphali* was found to be nearly twice as common as *lingnanensis*. Sampling during 1956 showed *chrysomphali* to constitute 91% of the *Aphytis* population present, and *lingnanensis* only 9%. There was no ready explanation for this apparent paradox, but rechecking of earlier plots revealed several other instances, all in mild coastal areas, where *lingnanensis* had originally been colonized and had become dominant at the expense of *chrysomphali* but now, several years after colonizations and regular studies had been terminated, *chrysomphali* was again predominant. In the more extreme climatic zones of the interior citrus areas *lingnanensis* remained by far the dominant species in all plots rechecked, and in certain coastal area groves it maintained dominance.

It should be borne in mind throughout this paper that we are dealing with the relative abundance of one species of parasite with respect to the other and not necessarily their abundance with respect to the host, *i.e,* the degree of biological control.

EXPERIMENTAL RESULTS AND ANALYSIS

The present study represents an analysis of laboratory data on the effects of competition and of temperature on *Aphytis lingnanensis* and *A. chrysomphali* grown in single as well as in mixed cultures in an attempt to help explain some of the anomalies in the observed distribution and relative abundance of these 2 species in the field. Previous studies have indicated temperature and sometimes humidity to be the most important factors limiting the abundance of single-species *Aphytis* populations in southern California (DeBach *et al.* 1955). However, these studies and the ones mentioned before (DeBach 1954) seemed to indicate that *lingnanensis* would be most successful in mild coastal areas; they gave little if any indication that *chrysomphali* would become dominant over *lingnanensis* in any locality.

For all practical purposes, both species of *Aphytis* are free of natural enemies of their own in California, except ants. Ants when present can seriously reduce the efficiency of both species (DeBach *et al.* 1951) either by direct predation or by interference. But there is no known differential effect acting between the 2 species of *Aphytis* or between localities; hence ants do not influence the major differences in distribution and abundance of *lingnanenis* and *chrysomphali,* with which we are concerned in this paper. Certain other parasites, as well as predaceous beetles which feed on the California red scale, on occasion offer a certain amount of competition to *Aphytis* for the host, but these other natural enemies operate at high host densities and largely disappear when and if the host population is reduced to a low level by *Aphytis*. In any event, these other parasites and predators have no differential effect on the two *Aphytis* species which could account for the observed differences in abundance of *chrysomphali* and *lingnanensis* in different localities. The only known factors which remain to influence the relative abundance of *lingnanensis* and *chrysomphali* within a given area or between areas are (1) meteorological factors and (2) competition between *lingnanensis* and *chrysomphali* for the host.

Test Procedures

Tests involving comparison between *Aphytis chrysomphali* and *A. lingnanensis* used as nearly identical techniques as is known to be possible. The parasites were cultured under identical temperatures and humidities on the same scale host (*Aonidiella aurantii*), which was cultured on the same plant host (lemon fruit). Essentially identical scale densities per lemon were used for testing purposes. Upon emergence, adult parasites were fed the same food (honey) and were otherwise handled identically previous to testing. The age of parasites and host insects was comparable in all tests. A constant relative humidity of about 58% was maintained in all cultures by the use of NaBr.

In order that the scale host remain in the stage most suitable for parasitism (the third-instar female), scale populations were subjected to a temperature of 40°F for 24 hours just before emergence of adult male scales. This treatment kills nearly all males and prevents fertilization of the female scales. As a result the females stay in the third instar indefinitely.

Biological Characteristics in Single-Species Cultures

Reproduction

Aphytis chrysomphali is a uniparental species in which the females give rise to females parthenogenetically, without the need for fertilization. Hence, no individuals are reproductively wasted as males. Uniparentalism is a distinct advantage to a well-adapted species.

Aphytis lingnanensis is a biparental species in which males are necessary for fertilization and the production of females. The sex ratio of individuals reared on the California red scale in the field is about 50:50. Actually, we obtained 47% females out of 788 individuals from 26 different field rearings. Thus, about half of the progeny of *lingnanensis* females do not reproduce themselves, and the effective reproduction or potential rate of increase is only about half of the total progeny. Therefore, if the total progeny per female *lingnanensis* is twice that of *chrysomphali,* the rate of increase of the two will be identical (other factors being equal) although *lingnanensis* will parasitize twice as many hosts as *chrysomphali.* If the total progeny per female were equal for both species, *chrysomphali* would hold a tremendous advantage, with twice the rate of increase of *lingnanensis* As shown later, however, the total progeny per female of *lingnanensis* under most conditions is substantially greater than that of *chrysomphali.* Uniparentalism in *chrysomphali,* however, serves to mitigate this disadvantage.

Effects of temperature

The data shown in Table I represent rates of development of *Aphytis lingnanensis* and *A. chrysomphali* as measured by the proportion of individuals that developed to the adult stage after given intervals at various temperatures and at a constant relative humidity of 58%.

TABLE I. Rates of development of *Aphytis lingnanensis* and *A. chrysomphali* from egg to adult at various temperatures and at a constant relative humidity of 58%

	% EMERGED AS ADULTS AT TEMPERATURE OF—			
	87°F		77°F	67°F
Species	After 12 days	After 15 days	After 17 days	After 22 days
A. lingnanensis	36	82	80	0
A. chrysomphali	47	100	100	43

These data show that *chrysomphali* has a shorter life cycle than *lingnanensis* at all temperatures tested (87°, 77°, 67°F). Previously published results (DeBach 1954, Table 7) gave fairly similar results at somewhat different temperatures. Both series of data indicate that *chrysomphali* possesses a greater relative advantage over *lingnanensis* at the lower temperatures than it does at the higher temperatures. It is significant that the localities where *chrysomphali* has exhibited dominance in the field possess relatively low mean temperatures. On the basis of these and other data on file it is estimated that in such areas *chrysomphali* may have as many as 2 to 3 more generations per year than *lingnanensis.* Other things being equal, this would confer a decided advantage upon *chrysomphali.*

The survival of adults in the field is of considerable importance in relation to the parasite's potential rate of increase. *Aphytis* adults lay eggs more or less daily throughout life, although about two-thirds of the total are produced during the first half of adult life. Conditions which depart from optimum not only reduce total oviposition by shortening the life span but also reduce the amount of oviposition during life.

TABLE II. Number of days required for adult females of *Aphytis lingnanensis* and *A. chrysomphali* to reach the LD_{50}, LD_{75}, and LD_{90} at various temperatures and at a constant relative humidity of 58%*

	A. lingnanensis			*A. chrysomphali*		
Temperature °F	LD_{50}	LD_{75}	LD_{90}	LD_{50}	LD_{75}	LD_{90}
67	53	58	67	69	89	93
77	25	28	36	32	35	43
87	12	16	20	16	25	27

* Food (honey) always available.

Table II shows the number of days required for adult females of *Aphytis lingnanensis* and *A. chrysomphali* to attain the LD_{50}, LD_{75}, and LD_{90} at various temperatures. At least 100 adult females were tested at each temperature. It is readily apparent that *chrysomphali* is appreciably longer-lived than *lingnanensis* at each temperature tested. This fact in itself would not prove that *chrysomphali* possesses any advantage, because total oviposition by *chrysomphali* could be small regardless of length of life. The important thing is whether longevity is differentially affected in the two species by departures from optimum or "normal" conditions. The 77°F temperature (Table II) would most nearly approach "normal" field conditions, and for this temperature it can be calculated from the data that the life of *chrysomphali* is about 25% longer than that of *linganensis; i.e.,* it takes about 25% longer for *chrysomphali* to reach the various mortalities shown (LD_{50}, LD_{75}, and LD_{90}). At the extreme temperatures, however, calculations show that *chrysomphali* lives about 41% longer at 67°F and about 42% longer at 87°F than *lingnanensis.* That is, *lingnanensis* suffers relatively more at the extremes than *chrysomphali* does, and it can be concluded from this that *chrysomphali* more nearly approaches its potential ovipositional capacity at the lower and higher temperatures than *lingnanensis* does.

The data in Table II do not agree with previous results (DeBach 1954), which indicated not only that both species were very much shorter-lived, but that *lingnanensis* was longer-lived than *chrysomphali.* It is believed that the improved testing techniques now used are responsible for the observed differences. The LD_{50} occurred so quickly in the former tests that it is now obvious that the general handling procedure in the earlier tests was very unfavorable to the parasites and that these earlier data should be evaluated accordingly.

Comparative tests were run on the total progeny produced by *Aphytis lingnanensis* and *A. chrysomphali* during one generation at 3 constant temperatures (67°, 77°, and 87°F) and 4 parental densities. The results are summarized in Table III. The relative rate of increase (or progeny per female parent), as used herein, permits comparison between the reproductive capacities of *A. lingnanensis* and *A. chrysomphali* females under different sets of conditions. The figures given under "progeny per female" represent the average progeny production during the life span of a female. In certain instances, especially at the highest temperatures, some second-generation progeny may be included. For the purpose of comparing the relative rate of increase of the species, this is considered to be inconsequential.

In order to analyze for the effects of temperature alone and to simplify presentation, the data of Table III were combined and averaged with respect to various densities. This gives a comparison between the effects of different temperatures at an average (more or less medium) parental density.

Table III. Effect of intraspecific competition at different densities and temperatures on progeny production (relative rate of increase) in single-species cultures of *Aphytis*

Density of parental females per lemon fruit	Mean Progeny Per Female Parent*					
	67° F		77° F		87° F	
	A. lingnanensis	*A. chrysomphali*	*A. lingnanensis*	*A. chryscmphali*	*A. lingnanensis*	*A. chryscmphali*
2	17.0	7.0	28.3	5.0	60.0	2 5
5	16.8	9.0	28.4	5.4	23.7	3.0
10	12.0	5.5	14.4	4.3	15.8	1.8
20	2.5	2.6	6.6	2.5	6.4	1.3

* Totals of 666 *lingnanensis* and 666 *chrysomphali* parent females were used to obtain mean progeny figures which represent emerged adult progeny obtained after allowing parental females to oviposit over a period of one generation at a constant relative humidity of 58%.

From the data in Table IV, several conclusions can be drawn. For *lingnanensis* alone it is evident that progeny production increases markedly from the low constant temperature of 67°F to the high constant temperature of 87°F. This would indicate that, other things being equal, *lingnanensis* should do better in the interior citrus areas, which have higher mean temperatures, than it would in coastal areas. For *chrysomphali* alone, the opposite trend is apparent. This species exhibits its highest progeny production at the low constant temperature of 67°F and its lowest progeny production at the high constant temperature of 87°F. This would indicate that *chrysomphali* should do better in the coastal citrus areas, which have lower mean temperatures, than it would in the interior citrus areas. These indications are amply borne out by many field studies and observations, particularly with respect to *chrysomphali*. Even before the introduction of *lingnanensis*, *chrysomphali* rarely became abundant in cirtus orchards in the interior areas.

Table IV. Effect of temperature on progeny production (relative rate of increase) of *Aphytis* species

Temperature, °F.	Mean Progeny Per Female Parent*	
	A. lingnanensis	*A. chrysomphali*
67	10.5	5.0
77	16.4	3.9
87	27.4	1.9

* Mean progeny figures obtained from tests using low, medium, and high densities of parent parasites. Each mean progeny figure is based on a total of 222 parent parasites which oviposited over a period of one generation at a constant relative humidity of 58%.

If the progeny production of the 2 species is compared for the 3 different temperatures, it will be seen that *lingnanensis* possesses a tremendous advantage in progeny production over *chrysomphali* at the high constant temperature of 87°F. At a constant temperature of 77°F, *lingnanensis* still possesses a marked superiority in total progeny production (about fourfold), but at the low constant temperature of 67°F the superiority is reduced to only about twofold. Since about half of the progeny of *lingnanensis* are males, the effective rate of increase as measured by progeny production is about equal for the 2 species.

Thus these limited laboratory tests give strong indications that under certain conditions of temperature *chrysomphali* has about the same intrinsic possibilities for progeny production as *lingnanensis*. It seems likely that certain low mean temperatures, other than those tested, would definitely favor *chrysomphali* over *lingnanensis* and that this indicates the major influence which determines that *chrysomphali* achieves superiority over *lingnanensis* in certain localities in the field.

Effect of intraspecific competition in single-species cultures

This study was carried out for 2 principal reasons, (1) to indicate how parasite density affects the rate of increase (progeny production) of either species, and (2) to serve as a basis for evaluating effects of parasite density when 2 species are competing for hosts. Only the effect of competition involving varying densities of individuals of the same species (intraspecific competition) will be considered here.

In these tests varying numbers of each species were placed in containers with scale-infested lemons bearing 250 to 300 host scales per fruit. Six scale-infested lemons were used per container and one container was used for each density of parent parasites and for 3 different temperatures. For present purposes, data from Table III for the 3 temperatures were averaged in order to simplify the presentation. Progeny production, *i.e.*, the number of F_1 adults in one generation, was the criterion.

TABLE V. Effect of intraspecific competition on progeny production (relative rate of increase) of *Aphytis* species

Original population density (No. of females per lemon)	MEAN PROGENY PER FEMALE PARENT*	
	A. lingnanensis	*A. chrysomphali*
2	35.1	3.8
5	23.0	5.8
10	14.1	3.9
20	5.2	2.1

* Data combined from tests run at 67°, 77°, and 87° F. Totals of 666 *lingnanensis* and 666 *chrysomphali* parent females were used to obtain mean progeny figures which represent emerged adult progeny obtained after allowing parental females to oviposit over a period of one generation at a constant relative humidity of 58%.

From the data summarized in Table V it is evident that the progeny per female of *lingnanensis* decreases drastically as the density of parent females increases. Progeny per female with an initial density of 2 females per lemon is nearly 7 times as great as with an initial density of 20 females. Total progeny production per lemon is even less with 20 parent females per lemon (104 total) than with 10 per lemon (141 total). These data indicate a high intensity of competition in *lingnanensis*. The factors involved in this competition have not been isolated and studied, but indications are that interference between ovipositing females is of greatest importance, competition between larvae (super-parasitism) and competition between adults for scales as a source of protein food being less important. In any event, the relatively great potential rate of increase of *lingnanensis* is damped considerably as population density increases. What this means in terms of field population dynamics is an open question.

In the case of *chrysomphali* the data show that competition is not the least at the lowest parental density but rather at an intermediate parental density. In these tests the optimum progeny production occurred with an original parental density of 5 per lemon which is greater than the minimum original parental density of 2 per lemon. This held true in all test series and appears to be significant although unexpected. If, as it appears, competition is less at some intermediate parental density, *chrysomphali* shows some benefit from slight crowding. At the higher initial parental densities (10 and 20 females per lemon) progeny production per female decreases but not markedly as with *lingnanensis*, so that total progeny production is greatest at the highest parental density (20 per lemon) tested. The females of *chrysomphali*, or their larvae, apparently do not interfere with one another very much even at high densities.

When it is recalled that about half the progeny of *lingnanensis* are males, then under conditions of heavy intraspecific competition (20 parental females per lemon), *lingnanensis* shows little advantage over *chrysomphali* in single-species cultures. At the lower parental densities, however, *lingnanensis* shows a much greater potential rate of increase than *chrysomphali*.

The data of Table IV shows that at a lower temperature (67°F) and an average density *chrysomphali* produced nearly as many female progeny as *lingnanensis*, and if we then superimpose the high density effects described above, we might expect *chrysomphali* to produce even more female progncy than *lingnanensis*. The original data show this to be the case. At 67°F and at the lower parental densities (2, 5, and 10 females per lemon), single-species cultures of *lingnanensis* and of *chrysomphali* produced about the same number of female progeny per parent female. However, at this low temperature and at the high parental parasite density of 20 females per lemon, *chrysomphali* produced about twice as many female progeny (2.6 per female) as *lingnanensis* (1.3 per female).

It can be concluded from these data that the much greater rate of increase exhibited by individual *lingnanensis* females, as compared to that of individual *chrysomphali* females, especially at higher temperatures, may be considerably less under conditions of intraspecific competition between individuals of the same species. At lower temperatures and a high degree of intraspecific competition, *chrysomphali* may even exhibit a greater relative rate of increase than *lingnanensis*.

The Effects of Competition in Mixed-Species Cultures

The foregoing data and discussions have enabled us to draw some conclusions as to the probable relative success of *lingnanensis* and *chrysomphali* under particular sets of physical conditions

Table VI. Effect of interspecific competition at different densities and temperatures on progeny production (relative rate of increase) in mixed-species cultures of *Aphytis*

Density of Parental Females Per Lemon Fruit			Mean Progeny Per Female Parent*					
	Species		67° F		77° F		87° F	
Total	*A. lingnanensis*	*A. chrysomphali*	*A. lingnanensis*	*A. chrysomphali*	*A. lingnanensis*	*A. chrysomphali*	*A. lingnanensis*	*A. chrysomphali*
2	1	1	11.2	3.7	38.5	2.5	113.0	1.9
10	5	5	5.8	5.2	15.7	2.6	20.5	0.6
20	10	10	5.9	0.6	11.3	0.1	16.3	0.1
5	1	4	6.6	6.0	32.3	4.8	60.0	2.9

* The 2 species cultured together in equal numbers. A total of 1998 parental females were used to obtain the mean progeny figures which represent emerged adult progeny obtained after allowing parental females to oviposit over a period of one generation at a constant relative humidity of 58%.

when each is exposed to various environmental conditions, but only where either species occurs alone. When they occur together, as they often have in the field, will the same results obtain, or will some added benefit accrue to one or the other owing to interspecific competition between adults or immature stages?

A number of selected tests were conducted in order to gain some insight into what might occur under what we considered to be most typical or most representative interspecific competitive conditions from the standpoint of trying to explain observed field results. These tests involved the use of equal numbers of parental females of each species in each container, except in one series where the ratio was 4 parental *chrysomphali* to 1 parental *lingnanensis*. Results were measured as progeny produced per female parent. The one series, which used more initial *chrysomphali* than *lingnanensis*, was included because *chrysomphali* represents the original established population in the field and, initially at least, usually outnumbered the numbers of *lingnanensis* colonized.

Table VI shows the relative rate of increase per female for each species, where the species occurred together under various combinations of parental density and temperature. In order best to interpret the effect of interspecies competition, comparison must be made with the results obtained from intraspecific competition in single-species cultures as shown in Table III. Only the parental densities of 2, 10, and 20 are strictly comparable between the 2 tables. A great many comparisons can be made between various combinations of the data in Tables III and VI. Only those most pertinent to the solution of the current problem are considered here.

Considering only the comparable parental densities of 2, 10, and 20 in Tables III and VI, it is evident that under conditions of intraspecific competition and at a low temperature of 67°F (Table III), *chrysomphali* (all female progeny) produced about as many female progeny as *lingnanensis* (50% male progeny) if not more at all parental densities. However, under interspecific competition at 67°F (Table VI), *chrysomphali* produced as many female progeny as *lingnanensis* or more at only one parental density (10). In single-species cultures (intraspecific competition) at 77°F and a high parental density (20), *chrysomphali* (2.5 female progeny) was nearly as productive as *lingnanensis* (3.3 female progeny), but in mixed-species cultures (interspecific competition) at 77°F, *chrysomphali* did not approach *lingnanensis* in female progeny production. At the high temperature of 87°F, *chrysomphali* suffered even more from competition with *lingnanensis*. It is also evident that *chrysomphali* suffers much more reduction in progeny production per female, especially at high densities, when competing with *lingnanensis* than when competing with equal numbers of its own species, and, conversely, that *lingnanensis* produces more progeny per female when competing with a given number of *chrysomphali* females than when competing with equal numbers of its own species.

These data indicate that when *lingnanensis* and *chrysomphali* occur together in equal numbers, *chrysomphali* will be as successful as, or more successful than *lingnanensis* only at low mean temperatures and at fairly low densities. However, if *chrysomphali* occurs initially in low but greater numbers than *lingnanensis*, as with 4 parental *chrysomphali* to 1 parental *lingnanensis* (see Table VI, at 67°F), there is some indication that *chrysomphali* will derive a relative advantage.

Discussion and Conclusions

The tests recorded herein were chosen as the most likely to afford data which might help explain why one species of California red scale parasite, *Aphytis chrysomphali*, remains more abundant in the field in certain localities in southern California than another red scale parasite, *A. lingnanensis,* with virtually identical habits, when most previous laboratory and field studies had indicated that *lingnanensis,* an introduced form, should largely if not completely replace *chrysomphali.*

Current studies of field distribution and relative abundance of these 2 *Aphytis* in groves in which *chrysomphali* was originally present and where *lingnanensis* was introduced several years ago, show that *chrysomphali* is frequently the more abundant parasite in coastal areas (sometimes to the near exclusion of *lingnanensis*) and that *lingnanensis* is the more abundant parasite in interior areas (often to the apparent exclusion of *chrysomphali*). The ability of *chrysomphali* to compete with and become or remain dominant over *lingnanensis* was first noticed in a mild coastal area near Santa Barbara, California, which has a rather low mean temperature for southern California but has less fluctuation between maximum and minimum temperatures, both summer and winter, than most other citrus areas. This led to a comparative laboratory study of the relative effects of low, medium, and high constant temperatures on both species. The 67°F constant temperature was chosen as the low because earlier studies indicated that this was within a few degrees of the developmental zero of the species involved, and this temperature also might serve as an index to what occurs in mild coastal areas. There is a considerable body of evidence, both field and laboratory, to indicate that temperature is the only important physical factor which influences the relative success of the 2 species in coastal areas.

Inasmuch as both species compete for identical requisites when they occur together, the effect of competition had to be studied.

We are now faced with the question as to whether or not the data and the discussion and conclusions already presented adequately explain or indicate why the observed field distribution and relative abundance of the 2 species occurs as it does.

The environmental factors studied have an effect on the number of F_1 progeny produced per parent female and, other things being equal, the logic seems inescapable that the species producing the most progeny under a given set of environmental conditions will become dominant and ultimately probably eliminate the other, inasmuch as they are competing for exactly the same requisites. The one catch in the previous statement is the phrase "other things being equal." Certainly we have not measured all ways in which climatic variations affect the progeny production of the 2 species involved, nor have we measured all their important characteristics. The one factor, other than those studied, most likely to influence relative success in the field is the relative searching ability of the parasite species—that is, their ability to find the host at low densities. Should one be much more successful in a given environment in finding hosts when they are scarce, it might predominate even though its potential progeny production per parent was less than that of the other. Unfortunately, we know of no satisfactory way of measuring searching ability in the laboratory. None of the tests reported herein, in which progeny per female parent was determined, involved searching, inasmuch as all host scales were available in a limited space. However, field observations indicate that the searching ability of the 2 species is not much different, if we use as a criterion the average density at which the host is regulated in areas favorable to one or the other species. Both can and do regulate populations of the California red scale at very low and similar levels under suitable environmental conditions. We have never considered one species to be a better searcher than the other. Therefore, it appears that the various factors analyzed in this study probably offer the best clues toward an explanation of the distribution and abundance of the 2 species.

The 6 major comparisons between the relative biological characteristics or abilities of *Aphytis chrysomphali* and *A. lingnanensis* are summarized below.

These results indicate that *chrysomphali* operates under great disadvantages with respect to *lingnanensis* at medium and high mean temperatures, which are indicative of those encountered in interior citrus climatological areas. However, at low mean temperatures, which are indicative of coastal climatological areas, the results indicate that *chrysomphali* is at its best biologically and *lingnanensis* at its poorest, and that the advantage, all things considered, lies with *chrysomphali.* It would appear, therefore, that the greater success of *chrysomphali* with respect to *lingnanensis* in certain coastal localities can be ascribed to the lower mean temperatures prevailing along the coast.

SUMMARY

It was concluded several years ago that the newly imported *Aphytis lingnanensis* would supplant *Aphytis chrysomphali* as the dominant parasite of the California red scale on citrus in south-

Advantages and Disadvantages

Biological characteristics	*Aphytis chrysomphali*	*Aphytis lingnanensis*
1. Sex ratio	All females	About 50% males. Progeny per female must be about twice that of *chrysomphali* to have same rate of increase.
2. Rate of development of immature stages	Faster than *lingnanensis*—as many as 2-3 more generations per year at lower temperatures	Slower than *chrysomphali*—fewer generations per year
3. Longevity of adults	Greater than *lingnanensis*—especially at higher and lower temperatures; enables closer approach to potential total oviposition	Less than *chhrysomphali*—tends to reduce possibility of obtaining potential total oviposition
4. Effect of temperature on female progeny production	Progeny production best at low temperatures, poorest at high temperatures, about equal to *lingnanensis* only at low temperatures	Progency production best at high temperatures, poorest at low temperatures; much superior to *chrysomphali,* at medium and high temperatures; about equal at low temperatures
5. Intraspecific competition	Increasing density exerts little effect on reduction of progeny per parent female; advantageous to *chrysomphali* at low temperatures	Increasing density greatly reduces progeny per parent female; however, progeny per parent female remains superior to *chrysomphali* except at low temperatures and high densities
6. Interspecific competition	Progeny production greatly inferior to *lingnanensis* except at low temperatures and low densities—then equal to or better than *lingnanensis*	Great superiority in progency production at medium and high temperatures and at high densities

ern California. Both laboratory tests and field population studies indicated this. However, it was learned later that *A. chrysomphali* had remained dominant in certain mild coastal areas over *A. lingnanensis,* sometimes even where *lingnanensis* had been colonized in large numbers. In an effort to explain this anomaly, laboratory studies on the effect of temperature and competition on progeny production by both species were conducted. They showed that *lingnanensis* possessed strong biological advantages over *chrysomphali* at the high temperatures of 87° and 77°F but that *chrysomphali* appeared to be equal to or better than *lingnanensis* at the relatively low temperature of 67°F. In so far as these constant temperatures may be an index to field conditions, the laboratory studies indicate that *chrysomphali* is better adapted to cool coastal environments and *lingnanensis* to hotter inland environments. This agrees with the known distribution of these species in the field.

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HABITATS AND SOURCES OF PLEISTOCENE MOLLUSKS AT TORREY PINES PARK, CALIFORNIA

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INTRODUCTION

Small assemblages of fossil mollusks are found in Upper Pleistocene marine terrace deposits of exposed-shore facies at Torrey Pines Park, San Diego County, California (Figure 1). Early descriptions of Late Pleistocene molluscan faunas from the Californian province, such as Arnold's classic monograph (1903), dealt chiefly with protected shallow-water facies. These latter facies, preserved in the lee of such Pleistocene islands as the Palos Verdes Hills, California, Point Loma, California, and the volcanic chain at Bahía San Quintín, Baja California, commonly contain large and varied assemblages. However, increasing attention has been given in recent years to the smaller assemblages of exposed-shore facies that are preserved chiefly on terrace remnants in the sea cliffs of headlands, as at Torrey Pines Park.

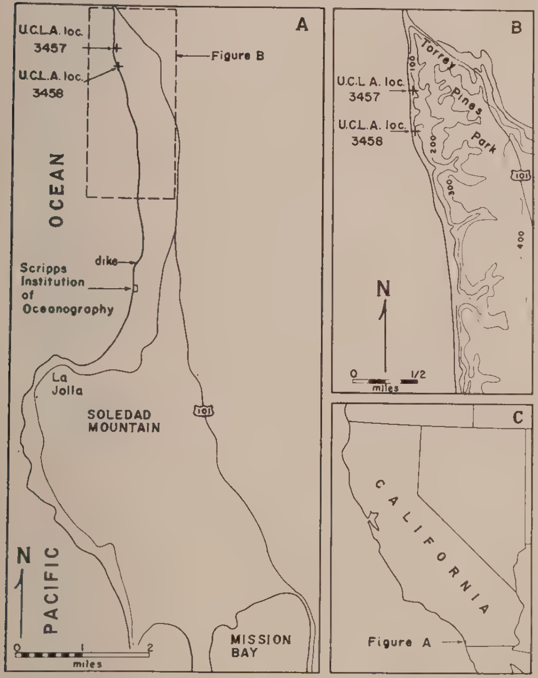

FIG. 1. Index maps of Torrey Pines Park, San Diego County, California, and vicinity, showing location of Upper Pleistocene fossil localities and of nearby sites mentioned in text.

Many exposed-shore Pleistocene faunas are now known from the Californian province, and they are rather similar. Most contain an element composed of species that live today only in the Oregonian province, from Point Conception, California and northward. As some of these exposed-shore facies grade laterally into deposits containing warm-water (Panamanian) species, the Oregonian element has been interpreted as indicating a local supply of cool water, probably from upwellings, on the south sides of points and along headlands (Valentine 1955, Emerson 1956). The chief differences between various exposed-shore assemblages seem due to changes in the kinds and numbers of species, derived from other habitats, that are intermixed with the exposed-shore forms. Yet, notable differences between just the rocky-shore elements of these assemblages are also found. They are probably due in large measure to differences in wave strength, steepness of shore, and nature of substrate, but these differences are not yet carefully worked out. However, the Torrey Pines Park assemblage differs from most other Late Pleistocene exposed-shore faunas in a particularly obvious way—it seems to lack the Oregonian element so characteristic of this facies.

A PLEISTOCENE THANATOCOENOSE FROM TORREY PINES PARK

Erosion of the sea cliff at Torrey Pines Park has nearly obliterated a marine terrace, but remnants of the terrace platform are preserved in the mouths of two hanging valleys (Figures 1 and 2; UCLA localities 3457, 3458). The shore-line angle of each of these terrace remnants is at an altitude of between about 65 and 70 feet, which suggests that the remnants are correlative with the Nestor terrace as mapped in the San Diego region and southward to the International Boundary (Ellis and Lee 1919, pl. 6). Fossiliferous marine sands and pebbly sands rest upon the terrace platform.

A short account of these deposits has been given by Stephens (1929, pp. 254-255), who noted the presence of 25 or more species and listed eight forms that he found to be most common (*Donax gouldi* is listed both as *"gouldii"* and as *"laevigata"* by Stephens). It is not clear which of the two localities recorded here was collected by Stephens; his description (". . . a mile or more south of the

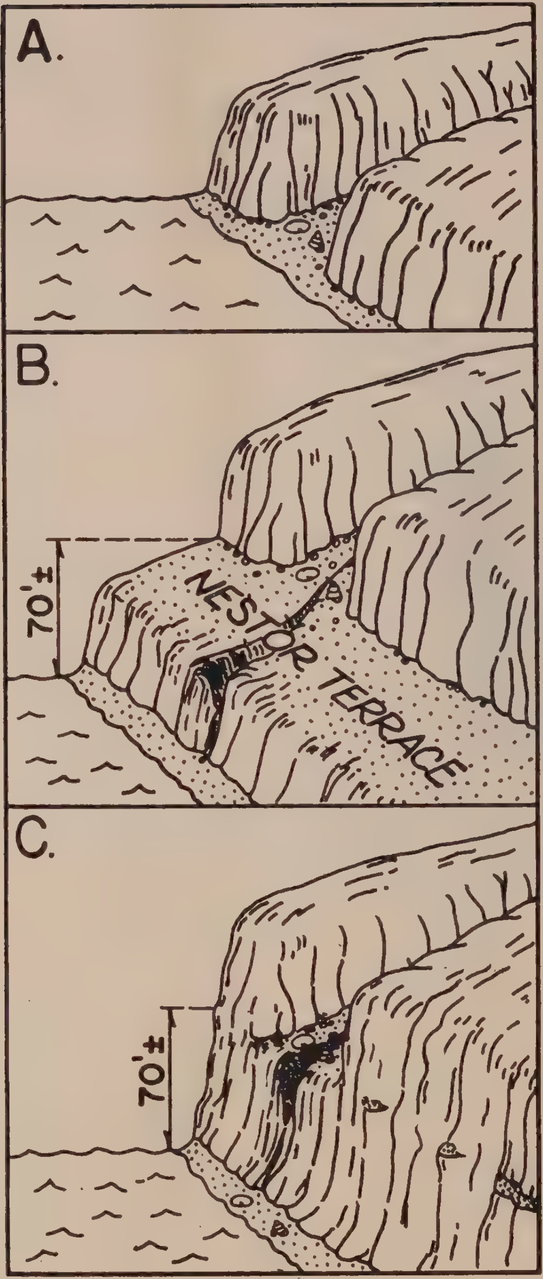

FIG. 2. Diagrammatic representation of three stages in the development of Pleistocene terrace remnants at Torrey Pines Park. (A), sandy beach backed by sea cliffs developed during high sea-stand on the Nestor terrace; mouth of creek is covered by pebbly beach sand containing shells. (B), establishment of sea level at present relative altitude, about 70 feet below the Nestor shore-line angle, and development of a sea cliff with base near present sea level; the Nestor terrace surface is veneered by marine sands. (The complicated history of land-sea relationships between stages A and B has been omitted as not pertinent to this discussion). (C), retreat of sea cliffs to present position, with preservation of Nestor terrace surface in mouth of hanging valley and on a few spurs.

northern end of the ridge") suggests the southernmost, but his map (1929, Fig. 1) indicates the northernmost.

The faunal lists presented here (Table I) are based upon collections by Gordon Wier (UCLA 2410), Drs. C. L. Hubbs and F. P. Shepard (UCLA 3459), and the writer at the northern locality (UCLA loc. 3457, Fig. 1), and by the writer at the southern locality (UCLA loc. 3458, Fig. 1).

These localities have yielded similar molluscan assemblages that total at least 74 forms (Table I, columns 1 and 2), of which 39 are gastropods, 33 pelecypods, 1 a scaphopod, and 1 a chiton. About 60% of the forms in each assemblage are characteristic of exposed rocky shore habitats today, and about 20% may represent shallow inner sublittoral communities. Three species live along exposed sandy shores, and the remaining species are rather wide-ranging ecologically. The most abundant species in the collections are those found along exposed shores, either rocky or sandy. As the terrace shore-line angle is only a few feet inland from the fossil localities, deposition must have occurred in very shallow water, or perhaps on the beach. Inner sublittoral forms, then, must have been washed inshore by waves. The association closely resembles Recent molluscan thanatocoenoses found along exposed rocky shores.

Most of the shells are rather badly broken and worn. Those representing an exposed sandy beach biotope are in the best condition as a group, but these are among the most robust shells in the collections, and the more solid and robust shells from other biotopes are fairly well preserved also. A few very delicate shells, such as *Lamellaria stearnsi,* have been preserved undamaged inside gastropod shells. Pelecypod valves are disarticulated. Shells in the Pleistocene assemblages are typically more broken and worn than those in the Recent assemblage discussed below, and were doubtless considerably worked by waves before final deposition.

A sandy beach is developed along Torrey Pines Park today; wave action is normally strong, although at times kelp beds appear offshore and damp the waves to some extent. The sea cliff is eroded in moderately soft sands of the Delmar and Torrey members of the La Jolla formation (Hanna 1926) and thus rocky shores are not developed. The terrace platform that bears the fossiliferous Pleistocene sediments is likewise eroded into these sands, and ancient sea cliffs that formerly

TABLE I. Pleistocene and Recent mollusks from Torrey Pines Park, California. The relative abundance of each species per 1,000 specimens collected is indicated by the following symbols:

2 or fewer	X
3 to 8	XX
9 to 32	XXX
33 to 128	XXXX
129 or more	XXXXX

	UCLA loc. 3457[1]	UCLA loc. 3458	Present beach at Torrey Pines Park[1]
Aletes squamigerus Carpenter	XXXX	XXXXX	XXXX
Donax gouldi Dall	XXXX	XXXX	XXXXX
Protothaca staminea (Conrad)	XXXX	XXXX	XXXX
Tivela stultorum Mawe	XXXX	XXXX	XXX
Fissurella volcano Reeve	XXXX	XXXX	XX
Olivella biplicata (Sowerby)	XXXX	XXXX	XX
Chama pellucida (Broderip)	XXXX	XXX	XXX
Saxidomus nuttalli Conrad	XXXX	XXX	XXX
Mytilus californianus Conrad	XXX	XXXX	XXX
Norrisia norrisi (Sowerby)	XXX	XXXX	XX
Zonaria spadicea (Gray)	XXX	XXXX	XX
Ostrea lurida Carpenter	XXX	XXX	XXXX
Conus californicus Hinds	XXX	XXX	XXX
Epilucina californica (Conrad)	XXX	XX	X
Cumingia californica Conrad	XXX		XX
Lucapinella callomarginata (Dall)	XXX		
Hipponix antiquatus (Linnaeus)	XXX		
Tegula gallina (Forbes)	XX	XXXX	
Pseudochama exogyra (Conrad)	XX	XXX	XXX
Trachycardium quadragenarium (Conrad)	XX	XXX	XXX
Hinnites giganteus (Gray)	XX	XXX	XX
Acanthina lugubris (Sowerby)	XX	XXX	
Platyodon cancellata (Conrad)	XX	XX	XXXX
Septifer bifurcatus (Conrad)	XX	XX	X
Diodora aspera (Eschscholtz)	XX	XX	
Haliotis cracherodi Leach	XX	XX	
Semele decisa (Conrad)	XX	XX	
Tegula funebralis (A. Adams)	XX	XX	
Crepipatella lingulata (Gould)	XX		XXXX
Neverita reclusiana (Deshayes) *s. l.*	XX		XXX
Pholadidea penita (Conrad)	XX		XXX
Astraea undosa (Wood)	XX		XX
Hipponix tumens Carpenter	XX		X
Haliotis rufescens Swainson	XX		
Ischnochiton acrior Carpenter	XX		
Navea? cf. *N. subglobosa* (Gray)	XX		
Tegula ligulata (Menke)	XX		
Trimusculus reticulata (Sowerby)	XX		
Amiantis callosa (Conrad)	XX	X	XXX
Petricola carditoides Conrad	XX	X	XXX
Bursa californica (Hinds)	X	XX	XX
Chione undatella simillima (Sowerby)	X	XX	XX
Schizothaerus nuttalli (Conrad)	X	XX	XX
Lucinisca nuttalli (Conrad)	X	XX	X
Pododesmus macroschisma (Deshayes)	X	XX	X
Pholadidea? sp.	X	XX	
Leptopecten latiauratus (Conrad) *s. l.*	X		XXXX
Crepidula onyx Sowerby	X		XXX
Acmaea digitalis Eschscholtz	X		XX
Tellina bodegensis Hinds	X		XX
Terebra pedroana Dall	X		X
Acmaea insessa (Hinds)	X		
Acmaea cf. *A. insessa* (Hinds)	X		
Acmaea sp.	X		
Amphissa versicolor Dall	X		
Chione picta Willett	X		
Cryptomya californica (Conrad)	X		
Dentalium neohexagonum Sharp & Pilsbry	X		
Diplodonta orbella (Gould)	X		
Glans subquadrata (Carpenter)	X		
Glycymeris cf. *G. subobsoleta* (Carpenter)	X		
Homalopoma carpenteri (Pilsbry)	X		
Lacuna carinata Gould	X		
Maxwellia gemma (Sowerby)	X		
Megatebennus bimaculata Dall	X		
Megathura crenulata Sowerby	X		
Mitrella carinata (Hinds)	X		
Neverita? sp.	X		
Parapholas californica (Conrad)	X		
Pusula californiana (Gray)	X		
Semele rupicola Dall	X		
Tegula aureotincta (Forbes)	X		
Transenella tantilla (Gould)	X		
Turbonilla tenuicula (Gould)	X		
Kelletia kelleti (Forbes)		XXX	
Littorina scutulata Gould		XX	X
Balcis cf. *B. oldroydi* Bartsch		XX	
Lamellaria stearnsi Dall		XX	
Turbonilla cf. *T. tenuicula* (Gould)		XX	
Plagioctenium circularis (Sowerby)			XXXX
Anomia peruviana d'Orbigny			XXX
Caecum californicum Dall			XXX
Crucibulum spinosum (Sowerby)			XXX
"*Nassa*" *fossata* (Gould)			XXX
Spisula dolabriformis Conrad			XXX
Tagelus californianus (Conrad)			XXX
Crepidula nummaria Gould			XX
Hiatella arctica (Linnaeus)			XX
Macoma secta (Conrad)			XX
Mytilus edulis Linnaeus			XX
Spisula catilliformis (Conrad)			XX
Thracia curta Conrad			XX
Zirfaea pilsbryi Lowe			XX
Barnea spathulata Deshayes			X
Calliostoma tricolor Gabb			X
Cingula sp.			X
Coleophysis harpa (Dall)			X
Ensis myrae Berry			X
Epitonium sp.			X
Gari californica (Conrad)			X
Jaton cf. *J. festiva* (Hinds)			X
Laevicardium substriatum (Conrad)			X
Macoma nasuta (Conrad)			X
Modiolus sp.			X
"*Nassa*" *perpinguis* Hinds			X
Pandora punctata Conrad			X
Pusula cf. *P. californiana* (Gray)			X
Tellina modesta (Carpenter)			X
Tricolia pulloides (Carpenter)			X
Turbonilla sp.			X

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[1] In addition to the mollusks, the echinoid *Dendraster excentricus* Eschscholtz and barnacles of the genera *Balanus* and *Tetraclita* were found at UCLA loc. 3457 and in the Recent beach assemblage.

backed the Pleistocene shore were presumably of the same general character as the present cliff. Thus it might be reasoned that the Late Pleistocene beach associated with the terrace shore line was sandy, and not rocky as the fauna suggests.

All the species represented in the Pleistocene collections are living today, although one, *Chione picta*, does not include the Torrey Pines Park district in its present range. It is known to be living from Bahía Magdalena, Baja California to Panama, and has been dredged from a depth of 6 to 7 fathoms on a sand and shell bottom (Hertlein and Strong 1948, p. 188). In the Upper

Pleistocene it is recorded in assemblages representing both protected and exposed shallow-water habitats from Pacific Palisades, California (Valentine 1956) to Bahía Magdalena, Baja California (Hertlein and Strong *loc. cit.*). Presumably *picta* indicates waters warmer than are common in the Torrey Pines region at present.

A Recent Thanatocoenose from Torrey Pines Park

UCLA localities 3457 and 3458 were collected on April 19, 1958 when the surf west of Torrey Pines Park was moderately heavy and the few preceding days had been stormy. Kelp beds were present offshore. Strewn along the foreshore and especially concentrated at the swash line were many shells of Recent mollusks. Although at other times wrack has been observed in transport to southward along this beach, these shells were being transported to northward. A collection from the swash line opposite UCLA locality 3458 contained 69 molluscan forms (UCLA locality 3974; Table I, column 3), of which 39 are probably identical with species in the Pleistocene collections. About 30% of the forms in this Recent thanatocoenose are characteristic of exposed rocky shores, and about 34% are characteristic of relatively quiet inner sublittoral habitats. Several of the more common forms—*Plagioctenium circularis, Crucibulum spinosum,* and *Tagelus californianus,* for example—are found associated today chiefly in sand and mud flats of quiet embayments, an association not represented in the Pleistocene collections. Three species live along exposed sandy shores, and the remainder range through several habitats. Only one species, the exposed sandy beach form *Donax gouldi,* was collected alive. Shells of species representing all these habitats were in excellent condition; for example, the periostracum of many specimens of *Mytilus californianus* and *M. edulis* was as intact as in life.

The precise sources of these varied faunal elements are speculative. About 2¾ miles south of Torrey Pines Park the present beach narrows; the sea cliffs, here composed of fairly resistant shales of the Rose Canyon member of the La Jolla formation (Hanna 1926) are awash at high tide and support a molluscan fauna that includes *Mytilus, Tegula, Acmaea, Littorina,* and chitons. To the south this splash-zone fauna grades into a rock-ledge and tide-pool association which is especially well-developed in the vicinity of a small dike that crops out about ¼ mile north of Scripps Institution of Oceanography. The pilings of the pier at Scripps also support *Mytilus* and associated mollusks. Still farther south, at La Jolla, exposed rocky shores are formed on hard Cretaceous sandstones. The rocky-shore species on the beach at Torrey Pines Park could have been derived from any or several of these localities. Many other forms, as *Chione undatella simillima, Tellina bodegensis,* and *T. modesta,* have evidently been washed ashore from usually quiet-water offshore habitats, perhaps from below 5 fathoms. The tidal-flat forms may have been transported from embayments well to the south, such as Mission Bay. Also a few forms, such as *Leptopecten latiauratus,* have probably come from the kelp beds.

Whatever the sources of these faunal elements may be, most of the species are not indigenous to the exposed sandy beach habitat in which they were collected. Only *Tivela stultorum, Amiantis callosa, Donax gouldi,* and perhaps the species of *"Nassa," Zonaria spadicea,* and a few others seem capable of living in shallow water along this beach.

Additional Considerations

Accumulations of storm-driven shells are often found well outside their normal habitats, and the occurrence at Torrey Pines Park beach is certainly not unique. Nevertheless it suggests a possible source for the dominant rocky-shore element of the Pleistocene assemblage—a source to the south, where relatively resistant Eocene and Cretaceous shales and sandstones doubtless formed rocky benches and tide-pools between Torrey Pines Park and Soledad Mountain (see Hanna 1926, map).

Along western Point Loma and northwestern Baja California are terraces that probably correlate with the Nestor terrace, and thus with the terrace remnants at Torrey Pines Park. These terraces have yielded exposed-shore assemblages that contain a few southern species, including *Chione picta* (Webb 1937, Valentine 1957, 1958). The assemblages also contain species of the Oregonian rocky-shore element mentioned above (*Tegula brunnea, T. montereyi, Amicula stelleri*), and are thought to represent regions where Late Pleistocene upwelling was effective in supporting such northern types. Perhaps the rocky shore from which so many species in the Torrey Pines Pleistocene seem to have been drawn was not consistently supplied with cool water. If the rocky-shore element has indeed been derived from the south towards La Jolla, it is reasonable to suggest that a relatively warm-water spot was present there at times during the Late Pleistocene —perhaps as a result of the piling-up of drifting surface waters to the north of the headland at Soledad Mountain.

SUMMARY

Although there is evidence to suggest that the Late Pleistocene Nestor beach at Torrey Pines Park was sandy, the molluscan assemblage associated with this beach contains a large exposed rocky-shore element. This rocky-shore element, unlike most other Late Pleistocene molluscan assemblages of this facies, lacks cool-water (Oregonian) species. Today the shore at Torrey Pines Park is sandy, but at times shells of rocky-shore mollusks, evidently washed from rock-cliffs, benches, and tide-pools to the south towards Soledad Mountain, may be found in abundance on this sandy beach. Perhaps the Pleistocene rocky-shore element was also derived from the south; if so, the lack of a cool-water element might be explained as a result of warm surface waters piling-up north of the Soledad Mountain headland.

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A BREEDING POPULATION OF THE MEXICAN TOAD (*BUFO VALLICEPS*) IN RELATION TO ITS ENVIRONMENT

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INTRODUCTION

This work was done to learn how a population exists in time under environmental oscillations. The Mexican toad was chosen for study because of ready availability of a study population and because it is a hygric-type terrestrial heterotherm with high potential natality. This toad ranges from Central America to southern Louisiana. Regional temperatures under which it occurs are moderate to mild, tropical, and regional moisture conditions range from excessive to sub-xeric. The local population studied lives near the northern limit of the range, where temperature might be suspected as a limiting factor and where rainfall is variable and often deficient.

Our population is a rather discrete one, located mostly on my property 5 miles east of Austin, Texas, on a Pleistocene terrace of the Colorado River. The local vegetation consists principally of cedar elm (*Ulmus crassifolia*) forest on the flood-plains of intermittent streams, open fields or mesquite (*Prosopis juliflora*)—prickly pear (*Opuntia lindheimeri*) brushlands on the uplands. Breeding of this population occurs mostly in an artificial pond ("tank") of about ½ acre. Some breeding usually occurs also in a gravel pit about 500 feet away across a state highway and in a very temporary rain pool west of it. In excessively rainy years some breeding also occurs in a shallow gravel pit about 200 feet from the tank and in a shallow, intermittent stream just below the dam that forms the tank. Individuals interchange among these breeding sites, but, other than these, there is no breeding site within ½ mile. There is minor interchange of individuals with populations as much as ½ mile away (Thornton 1954), but for the most part the population utilizing the sites mentioned above is a discrete breeding unit.

The toads were captured in the breeding pools, marked by toe-clipping, measured and released. Either an assistant or I marked and recorded the toads present on most nights of the years of the study. Field work with the population was initiated in August, 1951, when recently metamorphosed toads were marked to learn growth and survival rates (Blair 1953). The breeding population was studied by Thornton (1954) from 1950 through 1952; the present report concerns my own work from 1953 through 1958.

The 6 years over which the study has extended were notable for their extremes of rainfall and therefore provided an opportunity for assessing the behavior of the population under excess as well as extreme deficiency of rainfall. The average rainfall at Austin (1905-1957) for the 6-month period of March 1 to August 31, which is most important for the reproductive activities of the toads, is 17.30 inches. The rainfall in this period fell below average in 1953 through 1956, and in 1954 and 1956 it was very deficient with 7.46 and 6.20 inches, respectively. In 1957, there was an excess of moisture, with 28.24 inches in this period, and in 1958 the rainfall in this period was close to average.

Population Size and Structure

The total number of individuals marked in the breeding pools over a season is taken as the best estimate of the breeding population. Because of behavioral differences between the sexes, estimates made in this way are presumed to be more reliable for males than for females. The males stand small chance of being overlooked, because they can be located by their calls and because of their recurrence in the pools. A female, on the other hand, may be in the pool on only a few nights of the season and thus stands greater chance of being missed. Various of the toads marked in the pools were observed also in nonbreeding activity on watered lawns around the house. Only in 1958, as will be discussed later, was any considerable number of toads found there but not in the breeding pools. As will be detailed, changes occurred in the population through a breeding season. Some individuals disappeared, maturing young were added, and some probable immigrants from other populations appeared.

The total breeding population, without reference to sex, varied from a low of 97 individuals in 1953 to a high of 208 in 1957 (Table I). No estimate could be made for 1954 because the author was away and missed the single short period of breeding activity in that dry year. The largest population number was found in the wettest season but followed the driest season (1956). The population was smaller in 1958, although that season was one of average rainfall and followed the wettest season of all (1957).

Table I. Known numbers of Mexican toads (*Bufo valliceps*) in a breeding population located about 5 miles east of Austin, Travis County, Texas. No record is available for 1954 because the author was away and missed the short breeding season in that dry year

	♀♀				♂♂				
Year	Old	New	Total	% New	Old	New	Total	% New	Ratio ♀♀:♂♂
1953	19	14	33	42.4	23	41	64	64.1	34:66
1955	7	34	41	82.9	20	61	81	75.3	34:66
1956	9	11	20	55.00	28	54	82	65.8	20:80
1957	7	69	76	90.8	50	82	132	62.1	36:64
1958	5	7	12	58.3	11	143	154	92.8	7:93

Examination of the numbers of the 2 sexes separately gives a different picture than that afforded by the total population numbers. The number of males showed little variation in the years 1953, 1955 and 1956, but increased sharply in 1957 and increased again in 1958 to about 2.4 times the number recorded in the low year of 1953. The number of females increased sharply in the wet year of 1957, but unlike the males showed a drastic decrease in 1958.

All of the evidence points to an unbalanced sex ratio in the breeding population. This is viewed with caution because the males are more susceptible to detection than the females. Nevertheless, there is a considerable weight of evidence to indicate that males outnumber females in the breeding population. In 3 of the 5 years (Table I) the ratio of females to males was essentially 1:2 even though in these 3 years the total population varied from the low of 97 in 1953 to the high of 208 in 1957. This same ratio also shows in Thornton's (1954) numbers of breeding adults marked at this station over a 3-year period, 1950-52. He marked a total of 53 females and 107 males. Similarly, the number of females marked soon after metamorphosis that are known to have survived to sexual maturity was only half that of males (Table II). If a primary sex ratio of 1:1 is assumed, a differential survival of the sexes must be postulated to account for the unbalanced sex ratio in the breeding population. The mechanism whereby this might occur is unknown, but there is a reasonable hypothesis as to the ultimate value to the population.

Table II. Survival of known-age toads marked soon after metamorphosis in 1951

Number marked*	Alive after 1 year No.	Alive after 1 year %	Alive after 2 years No.	Alive after 2 years %	Alive after 3 years No.	Alive after 3 years %	Alive after 4years No.	Alive after 4years %
♂ 178	22	12.4	9	5.1	1	0.6	1	0.6
♀ 178	11	6.2	9	5.1	3	1.7	2	1.2

* Assumes 1:1 sex ratio at time of marking.

Males appear to be more vulnerable than females during the reproductive period, as they typically precede the females to the breeding pools and may call there on many nights. Furthermore, the calls would reveal the location of each male to any predator that was hunting by auditory stimuli. There would be an advantage, then, in the higher survival of the males to the period of reproductive activity. Turning again to the records of survival of known-age toads (Table II) there is evidence of greater attrition on males than on females after sexual maturity, although the numbers are too small to be conclusive. Only 9 (41%) of the 22 males that survived to maturity remained alive into their second breeding season, while 9 (82%) of the 11 females survived to their second breeding season. A similar differential is seen in the survival into the third breeding season.

The ratio of females to males in 1956 was only 1:4 but this may be related to the very short period of reproductive activity in that year. Our records appear to be a very good approximation of the number of females that bred in 1956, but the number breeding in the short period may not represent the total population of sexually mature females. The most remarkable departure from the 1:2 ratio came in 1958, when there was only one female recorded in the breeding pools for every 13 males. The difficulty in detecting all females in the various pools in which the population bred in 1958 might have contributed to this striking deviation, but we doubt that this effect was very important. For reasons to be discussed later, there seemed to be a discrepancy between the number of sexually mature females in 1958 and the number that actually reproduced. Eight adult females and 8 adult males were marked near the house in the period of April 25 to July 26, but these were never recorded in a breeding pool.

Some indication of the replacement in the population may be seen in Table I. Among males, 34 to 38% of the breeding population in 3 of the 4 years for which the computation could be made consisted of males that had been in the breeding population the preceding year. Only 1958 differed strikingly from this pattern, when, as a result of only 11 of the 132 males of the 1957 population remaining, and of a large increase in the number of yearling males, only 7% of the breeding population consisted of "old" males. The pattern of variation in replacement of females was much less consistent than in males. The absolute numbers of females surviving from one year to the next did not vary greatly, and the year to year variations in numbers of breeding females resulted mostly from variations in the number of previously unmarked females added to the population. The most striking variations were the large increase in "new" females in 1957 and the very small number of these in 1958, which largely accounted for the extremely unbalanced sex ratio in that year.

Many of the unmarked adults that appeared each year were obviously yearling toads that were participating in their first breeding season, and others were clearly more than one year of age. Others could not be classified as to year class because of the very considerable variations in growth rate (Blair 1953). An approximate separation into one-year-old and older classes can be made, however, by treating males less than 85 mm in snout-vent length and females less than 90 mm as yearlings (Table III). A toad first marked as a 2-year-old or older animal would necessarily be one that had been missed in records of previous years or that had immigrated. Very few unmarked males other than yearlings were found

Table III. Composition of the toad population in 4 years which followed years in which the population was marked. Females under 90 mm and males under 85 mm in snout-vent length arbitrarily classed as yearlings

	♀♀				♂♂			
	From previous year	Yearlings	Possible immigrants	Total	From previous year	Yearlings	Possible immigrants	Total
1953	19	7	7	33	23	36	5	64
1956	9	3	8	20	28	53	1	82
1957	7	42	25	76*	50	74	8	132
1958	5	5	2	12	11	143	0	154

* Includes 2 not measured and therefore unclassifiable.

in any year, but the number of previously unmarked, older females was relatively high. It is doubtful that this indicates a higher rate of immigration in females than in males, but it presumably indicates that considerable numbers of females failed to be recorded in the breeding pools in some years. The largest number of these older, previously unmarked females was found in 1957, following a year in which there was a single, short breeding period. We believe the number of females recorded in 1956 to be a close approximation of the number that actually bred in that year when others in the potential breeding population simply failed to reproduce.

A few of the toads lived a relatively long time. The longest-lived was a male marked as an adult, presumably a yearling, in 1950, and last recorded on April 29, 1957. This toad was approximately 8 years of age when he disappeared. On his last recorded date he was in the tank in amplexus with a female. Two years previously, on May 18, 1955, this male had an open sore on his left heel, with the left leg swollen, and a sore over the region of the right sacral diapophysis. These sores were healed when the toad was next seen on July 15, 1955, but the left heel joint was no longer movable. In his last 2 seasons, this male had a definite look of senility; among other things the skin was smoother and more tightly drawn than in younger toads. One female marked as a yearling in 1951 survived for at least 5 years. Among the known-age toads marked in 1951, 3 females survived for 3 years, and 2 of these survived for 4. One of the males survived for 6 years.

Reproductive Activity

One of the main objectives of this study has been to determine the distribution of reproductive effort through the potential breeding season in relation to environmental factors of temperature and rainfall. With this in view, the reproductive effort in 4 years, 1955-1958, will be considered in some detail.

The 1955 Season

The tank, which had dried completely in September of 1954, caught water during heavy rains of over 3 inches in early February, so this available breeding site existed prior to the time of expected breeding. Rainfall through the summer half of the year was below normal, with 12.62 inches, and in this period there were 5 rains of one inch or more.

The first reproductive activity of the season was seen on April 11, when a few males, and one female in amplexus with one of them, were found in the tank (Figure 1). This activity occurred on the third day of light rains, 0.42 inch on April 9, 0.19 on April 10, and a trace on the morning of the third day. The air temperature was 73° at 8 p.m. Temperatures of 70° or above at the same time of day had been recorded on various nights from February 26 to April 6, which would indicate that favorable temperature was not responsible for initiating reproductive activity. The light rainfall appears to have stimulated breeding. A fall of 0.59 inch on March 31 had failed to stimulate the toads for the apparent reason that the temperature had dropped to 58° by 8 p.m.

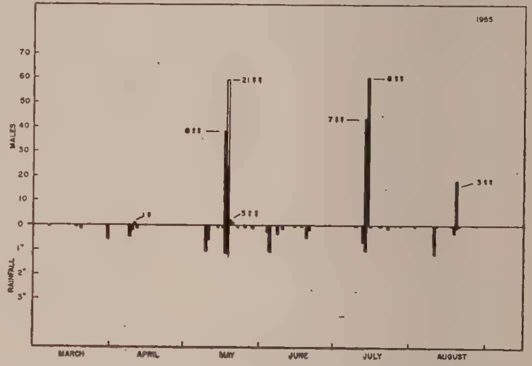

Fig. 1. Rainfall (below line) and repductive activity of Mexican toads (*Bufo valliceps*) in 1955. Rainfall from U. S. Weather Bureau records made about 2 miles away. Bars above line represent numbers of males in breeding pools; unshaded segment of bar in May represents males held captive from previous night and released after sample for night was captured. Females in pools indicated by numbers.

A peak of activtiy came on May 18 and 19, after early morning rains of over one inch on each day and with temperatures of 78 and 77° at 8 p.m. of the respective days. Another period of breeding occurred July 14 and 15, in conjunction with 0.70 inch of rain on July 13 and 1.04 inches on July 14. The air temperatures at 8 p.m. on the 2 days were 73 and 87°, respectively. The number of males was comparable with that of the May congress, but the number of females was smaller. A final, small breeding congress appeared on the night of August 20 following a local shower of one inch on August 19. This congress consisted of only 18 males and 3 females, of which only 2 were in amplexus. One of these laid eggs when kept captive overnight.

Forty-five (73%) of the 64 males present in the July 14-15 congress had also been present in May, and 7 of the 15 females had also been present. One of the females that had been present on May 19 in amplexus was in amplexus again and laid eggs on July 15. Seventeen of the 18 males and one of the 3 females in the August congress had been present in an earlier congress. This female was present in all 3 of the breeding congresses.

In summary, there were 3 breeding congresses in 1955, each of them following rainfall in excess of one inch and apparently stimulated by the rain. Each later congress was made up in large part of males that had participated in an earlier aggregation and to a lesser part by females that were known to have done so. All breeding pools, including the tank, were dry before the end of September, and it is doubtful that any eggs laid in the August breeding period resulted in metamorphosis.

The 1956 Season

The regional drought was severe in 1956, and there was only 6.20 inches of rain in the summer 6 months, with only one rain of over one inch in the entire period (Figure 2). All potential breeding pools were dry until there was a rainfall of 1.44 inches on February 8. The only rain of over one inch in the summer 6 months was one of 2.09 inches on May 1 followed by 0.83 inch on May 2. The only breeding aggregation of the year developed on May 1, with an air temperature of 63° at 8 p.m., and reached a peak on the following night, when the air temperature was 66° at 8 p.m. The aggregation of males on the night of May 2 was the largest recorded on a single night in the entire period of the study. In the absence of further rain, the breeding pools dried up, and the last of them, the tank, became dry on July 15 and remained so until December 18. The limitation of the breeding season in 1956 to a brief period in early May is attributable, then, to the lack of rain to stimulate reproductive activity and literally to the lack of any place to breed in the latter part of the season.

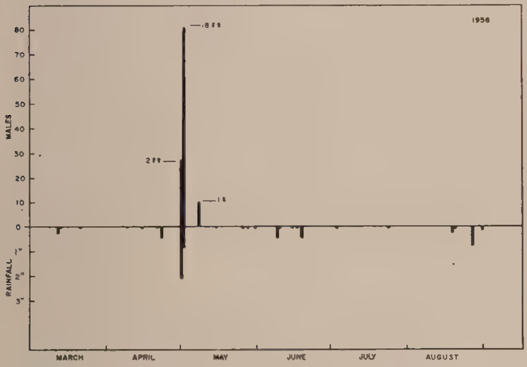

FIG. 2. Rainfall (below line) and reproductive activity of Mexican toads (*Bufo valliceps*) in 1956.

The 1957 Season

This was a year of excessive rainfall. The total for the year was 51.30 inches to be compared with an average annual fall of 33.33 inches and a fall of 15.41 inches in 1956. The summer 6 months had 28.24 inches, and there were 11 days with rainfall of more than one inch. The tank, which had caught water during 2.42 inches of rain on December 18 through 19, 1956, was overflowing or nearly so through the entire summer 6 months, and the other breeding pools were full except in late summer.

Breeding activity started on March 22 (Figure 3) following a rainfall of 1.64 inches on March 20.

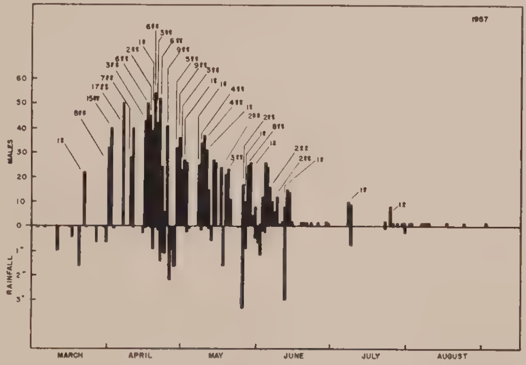

FIG. 3. Rainfall (below line) and reproductive activity of Mexican toads (*Bufo valliceps*) in 1957.

The air temperature had dropped to 58° by 8 p.m. on March 20 and to 64° on March 21. The temperature was 70° at that hour on March 22. Twenty-two males and one female made up the initial congress. The female laid during the night. A drop in temperature (58° at 8 p.m.) the following day stopped all activity, and there was no further breeding through 10 nights on which the 8 p.m. temperature was between 49 and 60°. Toads were back in the pools on April 1 and 2, when 8 p.m. temperatures were 74 and 73°, respectively. On the second of these nights, the second largest number (15) of females in the pools on any night of the year was recorded. The toads were absent, with the exception of one or 2 males, the following 4 nights, which had 8 p.m. temperatures ranging from 64 to 68°. On the next night (April 7) with an 8 p.m. temperature of 74°, there were 50 males and the largest number of females (17) recorded on any night of the year. The toads were inactive on the 2 following nights, which had 8 p.m. temperatures of 52 and 58°, respectively. Males, but no females, were present on April 10 and 11, when 8 p.m. temperatures were 66 and 68°, respectively. There was no breeding on the next 4 nights, with 8 p.m. temperatures ranging from 42 to 62°. Large aggregations were present on 9 nights of a 10-day period (April 16-25), when 8 p.m. temperatures ranged from 65 to 70°. The only small aggregation in this period was one of 6 males on April 24, when the temperature was 65°. Three days of cold rain with evening temperatures of 59 to 67° stopped all activity, but breeding started again on April 29, when the 8 p.m. temperature was 68°, and continued through 5 nights. There was another interruption of breeding from May 4 to 7, with evening temperatures of 60 to 64°. Another period of activity began on May 8, when the evening temperature was 72°, and continued through 4 additional nights with evening temperatures of 71 to 78°. There was no activity on May 13, which was cold and rainy, with an 8 p.m. temperature of 67°. Another period of activity extended from May 14 to 17, when evening temperatures ranged from 77 to 79°. A cold rain with evening temperature of 64° inhibited activity on May 18, but breeding aggregations appeared again on the nights of May 19-21, with evening temperatures of 74 to 82°. After this, activity slowed, and no more than one male was heard per night over 4 nights that had evening temperatures of 73 to 82°. A heavy rain (3.26 inches) on May 26 stimulated a period of breeding that tapered off on May 31. June 1 and 2 had drizzling rain, and there was no breeding. A rain of 1.16 inches on June 3 stimulated another period of breeding that tapered off by June 11. A rain of 3.03 inches on June 12 was followed by small aggregations of toads, but these were gone after June 15. Small numbers of toads appeared with light rains on July 8-9 and July 22-24. There was no rain in August. One male called on various nights between July 27 and September 1, but no aggregations were formed.

In summary, the 1957 season was one favorable to an extended reproductive season. Breeding aggregations were formed on favorable nights over a period of 86 days from March 22 to June 15, and, with the additional aggregations after showers in July, the breeding season extended over 125 days. In the early part of the season, breeding was interrupted several times by the passage of cool fronts which caused evening temperatures to drop below 70° F. The number of males in the breeding aggregations reached a peak just after mid-April and then declined. Rain showers played an important part in stimulating breeding activity. Breeding started on the first night with 70° evening temperature following a heavy rain. Toward the end of the main breeding season in late May and early June, 3 minor peaks of activity were attributable to the stimulus provided by rains of 1.16 to 3.26 inches, and the 2 aggregations in July were also attributable to rains.

Females were present in the breeding pools on 32 of the 56 nights on which there were aggregations of males in the 125-day period between March 22 and July 24. The largest numbers of females appeared in early April (15 on April 2; 17 on April 7), and by April 25 there had been recorded 52 of the 76 females recorded for the season. Thirty-nine of the females were recorded in the breeding pool only once, and 2 were never recorded there.

Thirty-five females were recorded in the breeding pools from 2 to 6 times each over periods ranging from 6 to 86 days. The appearance of a large fraction of the females in the breeding pools after they had once laid eggs shows that some females either remain in the vicinity of the pools after laying or that some spent females are attracted to the breeding aggregation. It also shows that at least some of the females may lay more than one set of eggs in an environmentally favorable season. The pattern of appearance of females in the pools is illustrated by the records of 20 females that were present on either April 1 or 2 and that were known to have laid on one of these dates. Sixteen of these were recorded in the pool at least one additional time in the period ending May 10. Nine of the 16 were recorded in amplexus a second time, and 6 of these were in amplexus on April 7, at which time they were surely spent. This behavior of the spent females is quite different from what we have seen in the laboratory, where a spent female, when clasped by a male, induces release by deflating the lungs and drawing the sides inward reducing her girth or by turning on her back. The only explanation of the field behavior seems to be that the stimulus of a large chorus of males, and possibly other factors not duplicated in the laboratory, leads the spent females to accept the males. Two of the longer records of females will be cited. Both of these had snout-vent lengths of 95 mm and are presumed to have been 2 years years old. One laid on April 1 and was found again in amplexus on April 7. She was found in the tank but not in amplexus on April 20, April 22, and May 9. She was found again in amplexus on May 28, but she did not appear to contain mature eggs, and there is no evidence that she laid on that night. The other female laid on April 2, and was found back in the tank on April 7 and 20. She was there again in amplexus on April 29 and on May 8; she did not appear to have mature eggs on either of these dates. One female definitely laid 2 sets of eggs. This female was in amplexus on April 29 and laid on April 30; she laid again on May 26 and was present but not in amplexus on July 8. The one female present on July 24 had laid on April 30.

The males were in the breeding pools much more frequently than were the females. On the average, a male was recorded in the pools on 9.8 of the 56 nights on which breeding aggregations were formed. Nineteen of the 132 males were recorded only on a single night, and 10 were recorded on only 2 nights over a span of 6 days or less. In view of the frequent recurrence of most males in the aggregation, it seems likely that most of these 29 males were taken by predators at the pools, although the possibility of movement away from the area cannot be eliminated. Two predators were seen taking males at the tank. These were a water snake, *Natrix erythrogaster,* and the bullfrog, *Rana catesbeiana.* It is not certain that the latter ever completely ingested a toad. In a few instances, a partly paralyzed bullfrog was found with a moribund toad in its mouth, and once a bullfrog in this condition was found near a mucous-covered, moribund toad that it had apparently tried to eat.

By April 25, 112 of the 132 males recorded in the season had been in the breeding pools at least once. Of the 20 males recorded after that date, 14 were small yearlings that evidently had not reached sexual maturity before the latter part of the breeding season. The aggregations formed in the latter part of the season consisted mostly of males that had been present in earlier aggregations, plus maturing yearlings and a few apparent immigrants. Some of the males were present in many of the breeding aggregations, and 2 were present on 37 of the 56 nights that aggregations were formed. One of these was in the first chorus of the year on March 22 and also in the last chorus on July 24. He was present in every aggregation from March 22 through April 22, but he was not found on April 23, 24 or 25. He was back in the next aggregation, on April 29 and was found in every chorus through May 11. After that time he appeared more sporadically, and in the latter part of the season he moved about among the tank, the gravel pit, and the intermittent streams below the dam. He was found in amplexus on April 29 and on May 28. The other male that was present on 37 nights was present in the chorus of April 1 and was also present in the last chorus of the season on July 24. This male was in amplexus on April 7. Like the other male, he moved about from tank to gravel pit and back in June.

Three others of the 8 males in the last chorus of the season (July 24) had been present in early April. One was first recorded on April 7 and appeared in aggregations on 20 nights. The 2 others showed quite different behavior. One first appeared on April 1 and was present on 10 of the 12 nights of breeding between then and April 22, but he was not seen again until he appeared in the chorus of July 24. The other appeared in 7 of the 8 choruses between April 7 and 20 and then disappeared until May 26, when he was in the gravel pit. Between that date and July 24, he was in 9 choruses in the tank, gravel pit or intermittent stream. The sixth male in the July 24 choruses was present on 23 nights between April 23 and that date. Two of the 8 males were unmarked. The records of the males indicate that not all of the local population of this sex moved to the pools on every night, particularly toward the end of the extended breeding season. This was indicated by other evidence, for on nights toward the end of the main breeding season males could sometimes be seen feeding under a yard light and apparently ignoring a chorus of calling males 200 feet away in the tank. The tendency to abandon the tank as a breeding site in favor of an intermittent stream and the gravel pit after about the first of June is of interest. The tank had taken on the appearance of a permanent body of water by this time, and it is possible that the toads preferred the rain-water pools at these other sites.

The 1958 Season

This was a normal season in amount of rainfall, with 17.45 inches in the summer 6 months. There were 5 rains of over one inch. The only important climatic deviation from normal was the lower than average temperature through the first 4 months of the year. The minimum daily temperature averaged 2.2° F. below normal in January, 3.2 in February, 4.5 in March, and 0.9 in April. In March, there was only one night on which the 8 p.m. temperature was as high as 70°, and the minimum on that night was 53°. In the first 2 weeks of April, the period in which the peak of breeding occurred in 1957, there was only one night with an 8 p.m. temperature above 70°, and in the entire month there were only 8 such nights.

The first small chorus of 4 males appeared on April 17, with an 8 p.m. temperature of 68° (Figure 4). This was 4 days after the first heavy rain (1.38 inches) of the year. Earlier appearance of the toads was probably prevented by low evening temperatures of 64 and 61°, respectively, on the nights of April 13 and 14, but the evening tem-

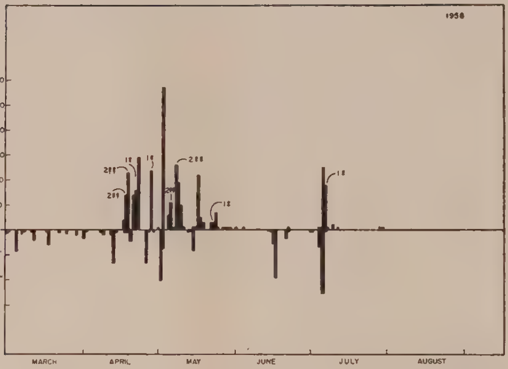

FIG. 4. Rainfall and reproductive activity of Mexican toads (*Bufo valliceps*) in 1958.

perature was 70° on April 15 and 68° on April 16. The number of males increased on the night of April 18, and 2 females, both of which laid that night, were also present. The number of males increased again the following night, but no toads appeared on April 20, which had drizzling rain in the morning and an 8 p.m. temperature of 68°. Choruses of males but only one female appeared in the period of April 21 to 23, with 8 p.m. temperatures of 76, 75, and 82°, respectively. A cool front ended this sequence of breeding activity, and no toads were present on April 24 to 27, when 8 p.m. temperatures were 63, 62, 69 and 73°, respectively. A chorus developed on April 28, with an 8 p.m. temperature of 77° and 2 days after a rain of 1.35 inches. Cooler weather again interfered, and no choruses were present over 4 nights that had 8 p.m. temperatures of 61, 55, 73, and 67°, respectively. The last of these days had 2 inches of rain, and the following day (May 3) had the largest aggregation of males of the year, but no females could be found. The next night was without breeding choruses, although the 8 p.m. temperature was 70°, and small choruses were present on the 6 following nights. A rain of 0.91 inch on May 15 stimulated a small peak of breeding activity that started on May 17 and lasted through May 24. A rainfall of 1.90 inches on June 17 caused no breeding activity. A rainfall of 2.52 inches on July 6 stimulated the last reproductive activity of the season.

The 1958 season differed remarkably from the others. This appears to be attributable in part to the abnormally cold Spring. It might also be attributable in part to changes in the principal breeding pool, the tank, as a result of more than a year of excessive rainfall. The entire shoreline of the tank had dense growths of vegetation (forbs, sedges and grasses), which in previous years were noted to be generally avoided by the calling males when there was a choice between barren shores and densely vegetated ones. Duckweed (*Lemna*) had appeared in the tank the previous summer, and in 1958 this and filamentous algae formed a complete vegetative mat over the pond. In previous years, the major breeding chorus formed in the tank, while minor choruses were sometimes formed in the subsidiary pools. In 1958, however, the choruses tended to be dispersed in the several pools available to the local population, and on a given night there might be more toads in one of these than in the tank.

Although more males (154) were recorded than in any previous year, these did not form large breeding choruses comparable to those of 1957, and on only one night, with 57 males, were more than 30 males recorded. There was also a great difference from 1957 in that the July 6-7 aggregation of 35 males included only 12 individuals that had been marked earlier in the season. This would imply a high turnover in the local population of males in 1958, either through mortality or movement. Sixteen of the 23 previously unrecorded males in the July 6-7 aggregation were definitely yearlings, which were possibly not yet sexually mature in the spring breeding season. Another unusual feature of the 1958 season was the finding of 8 males that were never recorded in the breeding pools. All but one of these was definitely a yearling, and the other one could have been of this age class. In addition, 6 immature toads ranging from 36 to 68 mm in snout-vent length were found, which was something that never happened in the other years. Another unusual feature was the failure of the males to form a breeding chorus after the rainfall of 1.90 inches on June 17.

The behavior of the females was equally as unusual as that of the males. No more than 2 females could be found in the breeding pools on any one night, and even on the night of peak calling by males no female could be found. A total of only 12 females was found in the breeding pools through the entire season, and none of these appeared there more than once. Futhermore, only 3 of these, two on April 18 and one on April 19, are known to have laid. Eight other females were marked away from the breeding pools, but never were found near the pools. The remarkably poor breeding season of 1958 is difficult to explain except as a possible result of the abnormally cold Spring. This conceivably could have upset internal reproductive periodicities of the toads.

Discussion

Natality is potentially much higher in these toads than in most terrestrial vertebrates. In round numbers a female will lay in the neighborhood of 20,000 eggs per set. The high natality in relation to the size of the breeding population is seen in the fact that survival of only one in 132 zygotes from a single set of eggs would have been adequate to account for the largest replacement observed (151 individuals in 1957).

Potential production varied greatly from year to year, as the reproductive effort varied greatly under limitations of the physical factors of rainfall and temperature. In even the year of lowest potential production (1958) the estimated production, assuming that all females found in the pools laid, was such that only one in 1600 zygotes produced would need to survive to give replacement comparable to that of the 2 previous years. At the other extreme, the new individuals in the 1958 breeding population represented the survival of only one in slightly over 10,000 of the zygotes estimated to have been produced in 1957. By contrast, the new individuals in the breeding population in 1957 represented a survival of one in 2650 of the zygotes estimated to have been produced in the relatively poor year of 1956.

Although potential production varied greatly from year to year as a result in part at least of climatic controls, the breeding population showed relatively little variation (97 in 1953 to 208 in 1957) through the period of drastic variations in moisture and rainfall. This is taken to indicate that the numbers of toads in the breeding population are regulated by density dependent factors. Just what the factors are is unknown, but it seems likely that a place to burrow where there is enough moisture to counter the water loss of these hygric animals may be the limiting factor. The increase in numbers in 1957 and 1958 (Table 1) is consistent with this theory, for the increase in ground moisture in those years should have increased the number of potential "homes." If this hypothesis is true, it follows that, in relation to current controversy in regard to density dependent versus density independent controls of numbers (Andrewartha and Birch 1954, Nicholson 1957), density dependent controls are operative, but the levels at which they are operative may shift in this case with a change in the regional weather pattern.

Summary

A local breeding population of the Mexican toad (*Bufo valliceps*) near Austin, Texas, was studied from 1953 through 1958 by toe-clipping the toads in the breeding pools. Rainfall was deficient in the first 4 years and extremely so in 1954 and 1956, and it was greatly in excess in 1957.

The estimated breeding population varied from 97 in 1953 to 208 in 1957. Males increased sharply in numbers in 1957 and 1958; females increased in 1957 but dropped sharply in 1958. The sex ratio appears to be unbalanced in the breeding population, with approximately 2 males for each female.

In 3 of 4 years, slightly over one-third of the males in the breeding population had been present in the preceding year, but in 1958 only 7% were carryovers from the previous year. The absolute numbers of females surviving from one year to the next varied relatively little, and the rather large variations in number of breeding females resulted mostly from variations in the number of new females added.

One male survived to an age of 8 years, and one female is known to have survived to an age of at least 5 years.

The amount and duration of reproductive activity varied greatly from year to year in relation to rainfall and to a lesser degree in relation to temperature. Rains of over one inch usually stimulated the formation of male choruses in the period from late March through August. Early evening temperatures below 70° F. usually, but not always, inhibited reproductive activity.

The peak of reproductive activity came in April or May, depending on the year. In 1955, there were late summer periods of activity in July and August, after rains of one inch or more. In 1956, there was a single short period of reproduction in early May, following the only rain of over one inch in the summer half of the year. In the excessively rainy year of 1957, the peak of breeding came in early April, but reproductive activity was spread over a period of 125 days from March 22 to July 24. Females appeared in the pools on 32 of the 56 nights on which male aggregations were formed. In the cold, rainy 1958 season, there were more males than in any other year, but few females appeared in the pools, and there was much less reproductive effort by the males than in the preceding year.

The same individual toads usually made up the breeding aggregations throughout an annual breeding season, although some individuals disappeared, some maturing young were added, and some possible immigrants appeared. Spent females sometimes reappeared in amplexus in the

pools, and a few are known to have deposited 2 sets of eggs in a single season.

The number of toads in the breeding population appears to be limited by a density dependent factor or factors. A place to burrow in which there is adequate moisture for survival is suggested as the limiting factor. The change from a drought regime to one of excess rainfall in 1957 may have shifted the level of operation of this presumed factor by increasing the number of potential "homes."

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AN ALTITUDINAL SURVEY OF REPRODUCTION IN *PEROMYSCUS MANICULATUS*

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Introduction

In eastern California a single subspecies of deer mouse, *Peromyscus maniculatus sonoriensis,* lives from 200 feet below sea level in Death Valley, Inyo County, to 14,247 feet above sea level on White Mountain, Mono County. This may be the greatest altitudinal range of any subspecies of terrestrial mammal. The present study was designed to compare the reproduction of local populations of this mouse at different elevations. Previous studies of the effects of altitude on reproduction have usually dealt with acute changes in oxygen tension rather than with possible long-range adaptations to different altitudinal environments. Such studies offer an incomplete picture of the total ecological effect of altitude on animals living in the wild. To assess this broad relationship requires a comparative study of established populations living naturally at different altitudes.

White Mountain, California, was chosen as the site for the present survey because of the proximity of populations of deer mice at high and low elevations and because of facilities offered by the White Mountain Research Station of the University of California. The research station served as a base for the field work, and the many courtesies that were extended to me by the station personnel enabled my field program to operate smoothly.

I wish to thank Dr. A. Starker Leopold, under whose guidance the project was conducted. My deepest gratitude goes to Dr. Oliver P. Pearson for his personal interest and help throughout the study. Financial assistance for field travel was received from both the Museum of Vertebrate Zoology and the Department of Zoology through their respective funds for supporting graduate student research.

Study Areas

The method of study was to trap deer mice at 4 elevations on the west slope of White Mountain and from these animals, taken periodically throughout the year, to reconstruct the annual reproductive cycles in mouse populations living at these altitudes. While "altitude" is the basis for comparison of the several populations, it must be remembered that there are many corollary differences in habitat involving climate, vegetation, and other factors. In the comparisons that follow, "altitude" implies the summation of environmental effects at any given level.

Area 1, elevation 4,500 feet (1,370 meters), was located at the mouth of Silver Canyon, almost at the level of the broad, arid Inyo Valley. Mean annual precipitation for nearby Bishop, California, is 5.76 inches, falling mostly during the winter months. Daily maximum temperatures normally run above 85°F throughout the summer (U.S. Dept. of Commerce 1956). Vegetation in Area 1 is sparse and composed mainly of such xerophytic low shrubs as *Atriplex* (2 species), *Chrysothamnus,* and *Artemisia tridentata.* Occasional willows grow along the stream which flows in an irrigation ditch in this area. Trapping was done mostly along the stream and in sites where sage (*Artemisia*) predominated. The driest, most open sites were found to be unsuited for *P. maniculatus.*

Area 2 was established at 7,100 feet elevation about 5 miles up Silver Creek from Area 1. The canyon here differs from the lower station in being much deeper with steep cliffs. Precipitation probably is greater and temperatures lower here, but weather data are not available. The north-facing slopes, where most of the trapping was done, are covered with open sage, *Chrysothamnus,* and occasional pines (*Pinus cembroides*). Streamside vegetation includes dense thickets of willow, alder, and wild rose. Snow does not accumulate to any depth at either of the two lower stations.

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Area 3, elevation 9,800 feet, was located on the north fork of Crooked Creek about a mile from the permanent White Mountain High Altitude Research Station. Here precipitation averages about 13 inches per year, mostly in the form of snow. The snow pack may accumulate to a depth of 2 or more feet during the winter months. Maximum summer temperatures reach the low 70's, while winter minima average around 15°F (Cook and Pace 1952). In the trapping area *Artemisia tridentata* composes almost 90% of the vegetation; other brush includes *Cercocarpus ledifolius, Chamaebatiaria,* and *Holodiscus*. Above the creek are open forest slopes of *Pinus flexilis* and *P. aristata.*

Area 4, elevation 12,400 feet, was situated near the Mt. Barcroft Research Station (Cook and Pace 1952). This wind-swept region, over 1,000 feet above local timberline, experiences a prolonged cold winter with snow accumulating several feet in depth. The growing season is consequently limited to a short summer period. There are some low bushes of *Ribes cereum* and *Chrysothamnus* growing near rocky outcrops, while grass (*Sitanion*) and such low forbs as *Trifolium monoense, Phlox* and *Polemonium* grow sparsely on the otherwise bare slopes. Sage, which provided the best habitat for deer mice at the lower 3 areas, does not occur on this highest study area. Running water is available from melting snow during the day from mid-spring to late fall, but there are no apparent stream courses. Trapping was carried out successfully in both the open areas and on the rocky sites wherever plant growth provided sufficient cover for the mice.

A fifth site, the summit of White Mountain (14,247 feet), was trapped on a single night to establish an altitude record for the mice, but data from the few mice captured are not included in this paper.

The 4 areas studied, all within an airline distance of 15 miles, are reasonably similar in vegetational habitat. All are located near running water, and none is forested. Open brush, mainly sage, characterizes the 3 lower areas, while plant life of the upper station is composed of typical arctic-alpine forms. Thus it is hoped that the influences of heterogeneous environments, other than those affected by altitude and its related weather, have been minimized.

METHODS

Field work

During the study, 559 *Peromyscus maniculatus sonoriensis* were trapped on the 4 study areas, as shown in Table I.

TABLE I. Numbers of mice examined at each area

Date	Area 1 elev. 4,500	Area 2 elev. 7,100	Area 3 elev. 9,800	Area 4 elev. 12,400	Total each trip
October, 1956	21	15	49	28	113
January, 1957	7	20	20	..	47
March, 1957	33	32	30	..	95
May, 1957	77	56	31	18	182
July, 1957	11	26	56	29	122
Total each area	149	149	186	75	559

Since the primary objective in trapping was to secure an adequate sample, traps were placed in the most promising *Peromyscus* habitat and were not spaced according to a set pattern. The bulk of the collecting was done with "Museum Special" snap traps baited with oatmeal or walnut meat, although, on occasion, a few Sherman-type live traps were used. In order to avoid trapping out the study areas, the trap lines were shifted locally during successive trips.

Each mouse was weighed, measured, examined for pelage condition, and autopsied. For males, length, color, the texture of the testes, length of the seminal vesicles, and size of the epididymides were recorded. For females, the following information was noted: vagina—open or closed (a few smears were made); mammary glands—relative size of nipples and whether or not milk was expressible; ovaries—number and size of corpora lutea and follicles; uterus—condition, size, number and size of embryos, number and appearance of placental scars; pelvis—interpubic symphysis open or closed. All tracts containing embryos were preserved in formalin for later sexing of embryos, where possible, and for detection of fetal resorption. In addition, the skull of each mouse was saved.

Aging by tooth-wear

Body weight, body length, and bone growth in small mammals exhibit a high degree of individual variation, sexual variation, and geographic variation (Howell 1924, Snyder 1954). It is difficult to age specimens accurately by these measurements of growth after the juvenile period of initial rapid development.

Although variation in degree of tooth-wear among small mammals has not been extensively studied, this method of aging individuals would seem theoretically to be excellent, presuming reasonable uniformity in the diet of the animals. Indeed, Hamilton (1940) has declared that tooth-wear, coupled with tooth color, is an infallible method of determining relative age in shrews. In the present study, since a small sampling of stomach contents from each area over the year revealed no striking differences in basic food habits of the mice, aging was done solely by tooth development and wear methods.

The technique adopted was similar to one described by Hoffmeister (1951) in his study of *Peromyscus truei*. Fifteen age groups were established to include a complete range of tooth-wear in order of increasing wear of the upper molars (Table II). Degree of eruption of the third molar was also considered in setting up the youngest groups. Representative skulls, one for each group, were permanently fixed, teeth up, on file cards to form a series of ascendency of tooth-wear groups. Using this series each unclassified skull could with little difficulty be assigned to a group by comparison. Patterns of wear differ somewhat among individuals (Hooper 1957), but wear was found to correspond closely to the definition set up in Table II.

Assuming that tooth-wear is a valid indication of age, it is useful to assign approximate chronological ages to the tooth groups. This has been done in Table III after considering the following factors:

TABLE II. Tooth-wear descriptions

Group	Description of stages of tooth-development and tooth-wear
1	M^3 not visible to $\frac{1}{3}$ erupted
2	M^3 $\frac{1}{3}$ to $\frac{3}{4}$ erupted
3	M^3 $\frac{3}{4}$ to fully erupted but shows no wear
4	M^3 shows light wear
5	M^3 cusps worn to three main loops
6	M^3 worn to single lake but paracone prominent; M^{1-2} lingual cusps slightly worn
7	M^{1-2} lingual cusps about $\frac{1}{2}$ worn; slight labial wear
8	M^3 worn smooth except for paracone; M^{1-2} lingual cusps more than $\frac{1}{2}$ worn to base
9	M^{1-2} lingual cusps worn nearly smooth
10	M^2 labial cusps worn about $\frac{1}{3}$ to base; slight M^1 labial wear
11	M^2 labial cusps worn about $\frac{1}{2}$ to base; M^1 labial cusp wear about $\frac{1}{3}$
12	M^1 labial cusps worn about $\frac{1}{2}$ to base; anterocone nearly smooth
13	All molars worn nearly completely smooth; M^2 lakes joined
14	M^2 reentrant angles nearly obliterated; M^1 reentrant angles present
15	All teeth completely smooth; all reentrant angles obliterated

TABLE III. Chronological age assignments for tooth groups based on factors other than tooth-wear. Numbers represent averages for each factor expressed in days

tooth group	weight	length	pelage	female reproduction	male reproduction	White Mtn. frequency distribution	FINAL ASSIGNMENT age in days
1	22	21					0-25
2	28	33					26-32
3	36	35	29				33-35
4	38	39	35				36-42
5	44	45	45	49	51	61	43-57
6			55	74	60	97	58-92
7				105		123	93-160
8						149	
9						250	
10							
11							1 year to 15 months
12							
13						17 months	
14						21 months	about 2 years or older
15							

1. Body weight and body length. Mean weights and lengths for each tooth-wear group were calculated and compared with the growth curves of known age specimens of *Peromyscus maniculatus sonoriensis* (Dice and Bradley 1942). The second and third columns of Table III show the average age of Tooth Groups 1 through 5 based on the Dice and Bradley growth-age curves. Comparisons of White Mountain individuals with laboratory mice for older age groups are not considered reliable.

2. Pelage. Column 4 of Table III was calculated by comparing proportional numbers of juvenal, sub-adult, and adult pelages for each White Mountain tooth group with published records of the age at molt (Collins 1923, McCabe and Blanchard 1950, Snyder 1956).

3. Reproductive maturity. The age correlations in columns 5 and 6 are based on the average ages at which male and female reproductive maturity is reached (Clark 1938, Jameson 1953).

4. Tooth group frequency distribution. Finally, chronological ages estimated by the preceding methods were extended to older tooth groups through examination of the frequency distributions of tooth-wear groups obtained on successive trips to each area (column 7). Thus, if the mode of the tooth group distribution for a single area was

Group 3 for the first trip, and the mode had advanced to Group 7 for the second trip, 89 days later, the difference in age between Group 3 and Group 7 would be 89 days, and Group 7 would be assigned an age of 123 days (34 days, the average age of Group 3 based on the other factors discussed above, plus the 89 day interval).

After considering all the above factors a final age assignment was designated for each tooth group, and this appears as an age range in the last column of Table III. These age designations are most reliable for the youngest tooth groups and should be considered only as approximations for the older groups. When compared with other age-dependent factors such as weight, body length, pelage, and reproductive conditions, as well as date of capture, the degree of tooth-wear seemed to be in good accord with the other combined factors.

Reproduction

The reproductive system of *Peromyscus* is similar anatomically and physiologically to that of the house mouse, which has been described by Snell (1941). The estrous cycle lasts 4 to 6 days, and ovulation occurs spontaneously during the middle or last part of estrous (Clark 1936). Gestation varies from 21 to 40 days depending upon concurrent lactation and other factors, while lactation lasts from 22 to 37 days (Svihla 1932). Post partum breeding probably represents the most frequent condition during the breeding season in the wild (Jameson 1953).

Jameson (1950) has shown that whenever the tubules of the cauda epididymis are so swollen as to be clearly visible to the naked eye in *P. maniculatus,* the epididymis contains spermatozoa. Following Christian's (1950) method, a sample of epididymal smears was taken in the present study; examination of these smears confirmed Jameson's findings. Therefore, condition of the epididymis is used here as the main criterion of male reproductive condition. All epididymides of intermediate size (barely visible to the unaided eye) were smeared, and whenever at least 20 spermatozoa per 1.35 mm diameter field could be counted under the microscope, that male was designated as being in breeding condition.

Females were considered to be in breeding condition if they were pregnant or lactating, or if they exhibited an open vagina, fresh corpora lutea, or a turgid uterus. There was no indication that altitude had any bearing on the basic progression of the normal female cycle.

Age of potential adulthood

In comparing breeding populations, it is useful to detect any possible differences in the age at which both males and females become reproductively mature. In laboratory stocks of *P. maniculatus* sexual maturity is reached by the average male and female at about 50 days of age (Clark 1938). It has been proposed that this is true also for wild deer mice (Blair 1940). In the White Mountain population, Tooth Group 5 (43-57 days) was the youngest group that included mature male mice, and males in breeding condition belonging to this tooth-wear class were captured from each of the 4 elevations trapped. Tooth Group 5 was also found to be the youngest group in which females were in breeding condition. Therefore it is assumed that mice of either sex may be potentially mature if they show tooth-wear of Group 5 or greater. Hereafter the term "adult" will be used to mean any mouse in Tooth Group 5 or older.

Based on tooth-wear, there was no evidence of altitudinal difference in the average age at which mice on White Mountain reached sexual maturity. Young mice matured at the same age during the breeding season regardless of the stage of the season, whether early or late.

The breeding season

The breeding season is here defined as that period from the date on which the oldest juvenile would have been conceived to the birth date of the smallest embryo in any single interval of breeding activity. Figure 1 shows the periods of reproduction among mice of the 4 field stations. Since collecting trips were made at intervals of 2 to 3 months, the full duration of the breeding season could not be determined solely from pregnant and lactating females captured. However, breeding that may have taken place prior to each of the trips could be ascertained by the occurrence of young mice in that sample. In Figure 1 both these direct and indirect evidences of reproduction are shown. Evidence of previous breeding based on mice in Tooth Groups 1-3 (ages 0-35 days) is shown separately from that based on mice in Groups 4-6 (ages 36-92 days), since more confidence can be placed in the aging of younger specimens. Mice older than Group 6 were not considered for breeding season estimates.

In Figure 1 note that the lower 2 elevations seem to be characterized by a split breeding season, with activity in both spring and fall, but with a drop off in summer and winter. However, at these lower stations the presence of mice younger than 2 months old in samples throughout the

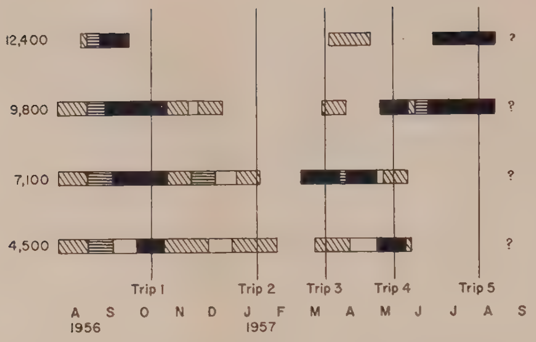

FIG. 1. Evidence of breeding in mice living at various elevations. Black bars based on observed pregnant or lactating females. Hatched bars based on age of young mice as determined by tooth wear: age groups 1 to 3, horizontal hatch; age groups 4 to 6, diagonal hatch. Vertical lines represent sampling dates.

year (see Figure 2) indicates that breeding may take place sporadically during the winter months. The same general pattern of breeding has been reported for *P. maniculatus* elsewhere (*e.g.* Jameson 1953).

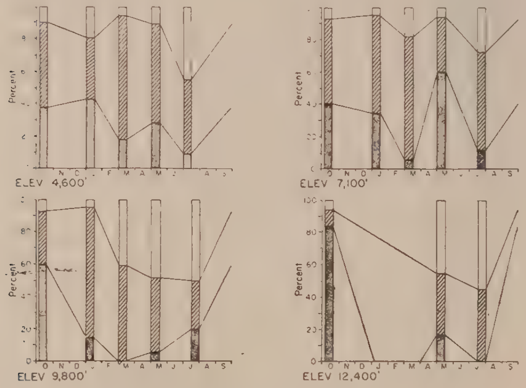

FIG. 2. Age structure of mouse populations at various elevations, based on seasonal trapping samples. Age categories depicted are: dotted bars, under two months; hatched bars, two months to one year; open bars, over one year of age.

The upper 2 elevations on White Mountain were characterized instead by a single main breeding season during the summer with no indication of mid-winter reproduction. Samples were not taken from the 12,400 foot station on the January and March trips because of snow and cold, but it may be assumed that if the mice failed to breed at the 9,800 foot level during winter months, this static condition also prevailed higher on the mountain. However, in the May sample 6% of the mice from 9,800 feet and 17% of the mice from 12,400 feet were less than 2 months old (Fig. 2—all these were in Tooth Group 5) suggesting that even at these greater altitudes some sporadic breeding may take place in March or April. The White Mountain records do not agree with those of Hawbecker (1955) who found no sexual activity in *P. maniculatus* in the Sierra Nevada at 9,800 feet during August.

It seems logical that the breeding season was shortest at the highest area. At 12,400 feet the season was probably not over 4 months in duration, at 9,800 feet it may have extended over a period of more than 5 months, and the aggregate of breeding periods in a year was apparently even greater at the lower elevations.

Litter size

Of the 559 *P. maniculatus* trapped, only 40 were pregnant females. Therefore, conclusions as to litter production and prenatal mortality are limited by the small size of the sample. Table IV summarizes the average litter size by altitudinal station. Potential litter size (column 5) is estimated by counting the corpora lutea or the embryo sites, whichever is greater, since more embryos than corpora lutea indicate that polyovuly or polyembryony has occurred. Potential litter size seems to be greater for the higher elevations. Mean number of observed embryos (including resorbing embryo sites) for pregnant females, fresh placental scars for non-pregnant lactating females where scars could be clearly distinguished, and a combination of these 2 groups are shown in the fourth column. Since no questionable counts were included, it is felt that scar counts were a reliable indication of previous embryos in lactating females. Scars older than recent sets in lactating mice were not used in this survey, as old scar counts have been shown to be unreliable (Davis and Emlen 1948). Comparing the mean

TABLE IV. Relative litter size and mortality. Each sample is expressed as a mean plus or minus its standard error. Scar counts are for lactating non-pregnant females. N is the number of females in each sample

elevation	basis of count	N	embryos or scars, (all sites included)	potential litter size	healthy embryos only	% resorption
12,400′	embryos	8	4.75± .16	4.88± .46	4.63± .38	2.6%
	scars	5	4.80± .37			
	emb. + scars	13	4.77± .19			
9,800′	embryos	19	4.84± .25	5.06± .16	4.01± .35	17.4%
	scars	17	4.71± .10			
	emb. + scars	36	4.77± .17			
7,100′	embryos	11	4.54± .36	4.73± .67	3.64± .68	20.0%
	scars	4	3.00 ..			
	emb. + scars	15	4.14± .26			
4,500′	embryos	2	4.00±1.00	4.00±1.00	4.00±1.00	......

scar and embryo counts for the 4 elevations, there seems to be an increase in average number of sites from the lowest to the highest elevations. The difference between the 7,100 foot area and the upper 2 stations approaches statistical significance.

When only healthy embryos are counted, the litter size is smaller, but the gradient with altitude remains (column 6, Table IV). In fact, the apparent post-implantation, pre-natal mortality decreased with increasing altitude (column 7). Note that the lowest area provided only 2 pregnant mice; therefore, the results for this area, apparently inconsistent with trends for the other 3 elevations, are completely unreliable.

Sex ratio

Sex ratio has an important bearing on the reproductive potential of a population, since this potential will be governed by the number of adult females during the breeding season. Changes in sex ratio with age would also influence the breeding potential. Table V shows that males outnumbered females at each elevation. Although a difference in aggregate sex ratios between areas is apparent, the difference is not significant at the 95% confidence level. The Brant and Snedecor method of computing Chi-square was used here (Snedecor 1956). Table V also shows that the sex ratio did not differ significantly among the 3 age classes compared. This stability of sex ratio following birth implies that post-natal mortality is independent of sex.

There was, in addition, no apparent change in sex ratio with time of year. However, sex ratios for these mice do vary from year to year, for Hoffmann (1955), snap-trapping *P. maniculatus* on White Mountain during a population high in 1954, captured 141 males and 340 females, a result strikingly different from my over-all ratio of 332:227.

Population dynamics

It has been shown that the total duration of the breeding season decreases with increasing altitude and that litter size tends to increase. Actual reproductive rates could not be determined directly, since it was not known how many litters were produced per female in each year. In stable populations, however, realized breeding success will be inversely proportional to average longevity, which may be determined from sample age structures. For example, Figure 2 suggests that the populations from the upper areas are composed of older animals on the average. To reduce theoretical breeding rates and mortality rates for a single year from known age structures, one must assume that mortality is independent of age, that breeding and mortality rates remain fairly uniform from year to year, and that trapability is independent of age. Wild populations are doubtless characterized by none of these attributes, but for the purpose of the present study in which 4 different populations are being compared, it seems likely that these variables would not obscure basic differences between the populations.

TABLE V. Sex ratio of trapped specimens per area broken down into three age classes. Trips have been combined for each area

	TOOTH GROUPS 1-4			TOOTH GROUPS 5-10			TOOTH GROUPS 11-15			AGGREGATE		
elevation	♂	♀	%♀	♂	♀	%♀	♂	♀	%♀	♂	♀	%♀
12,400′..........	12	10	46%	17	10	37%	16	10	39%	45	30	40%
9,800′..........	21	8	28%	54	43	44%	42	18	30%	117	69	37%
7,100′..........	9	13	59%	59	49	40%	9	10	53%	77	72	48%
4,500′..........	8	5	39%	74	44	37%	11	7	39%	93	56	38%
Aggregate.......	50	36	42%	204	146	42%	78	45	37%	332	227	40%

TABLE VI. Age structure of samples, males and females combined, trips combined. Number of mice and the corresponding percentage for each age class are given

	(0-1 year)		(1-2 years)		(more than 2 years)	
elevation	a	%a	b	%b	c	%c
12,400′......	49	65	17	23	9	12
9,800′......	125	67	47	25	14	8
7,100′......	131	88	13	9	5	3
4,500′......	131	88	17	11	1	1

To compute breeding rates and post-natal mortality rates, the population samples were broken down into one-year age classes. Data in Table VI include all samples taken over the year for each area; such lumping is valid when dealing with age classes with an interval of one year. The percentage of young in the population may be used as an index of breeding rate. This percentage (M) is computed as follows:

$$M = \frac{\text{number of first year mice in sample}}{\text{total number in sample}}$$

If populations remain balanced from year to year, M will also represent the annual mortality rate, and this has been tabulated in Table VII as a percentage for each area. Annual survival rates will be 1—M (Table VII, column 3).

The calculated number of young produced annually per adult can be expressed by M/annual survival rate, and the number of young produced per "unit adult female" is computed by dividing the above by the percentage of females in the

TABLE VII. Data on population dynamics computed from age structure

elevation	post-weaned mortality rate	post-weaned survival rate	young per unit adult	young per unit adult female
12,400′......	65%	35%	1.9	4.8
9,800′......	67%	33%	2.0	5.5
7,100′......	88%	12%	7.3	15.2
4,500′......	88%	12%	7.3	19.2

TABLE VIII. Trapping success per area, trips combined

elevation	trap nights	*Peromyscus maniculatus*	% success per trap night	% success other seed eaters per trap night
12,400′.....	1399	75	5.4	0
9,800′.....	2292	186	8.1	0
7,100′.....	1217	149	12.3	30.9
4,500′.....	2323	152	6.5	19.1
aggregate...	7231	562	7.8	....

population and multiplying by 100 (Table VII, column 5). The term "young per unit adult female" should be thought of as an average reproduction rate for the entire population of adult females rather than as an average production per female, for some adult females may fail to bear young, and others may produce more than one litter during their first year of life. The real significance in the computation lies in a comparison of the 4 areas. It is seen that the actual breeding rate at the lower 2 elevations must be more than 3 times that at the upper station. Mortality must differ correspondingly.

Actual breeding and mortality rates are expected to be higher than those tabulated, since few unweaned individuals would be included in the sample. Mortality before weaning is probably more than 20% (Howard 1949).

Population density

Table VIII records trapping success at the 4 elevations. From the table it may be inferred that deer mice were most abundant at the 7,100 foot area and least abundant at the upper and lower elevation extremes. Other seed eating rodents were also most common at 7,100 feet (last column, Table VIII). These possible competitors for food included *Peromyscus crinitus, Reitherodontomys megalotis, Perognathus formosus, P. parvus,* and *Dipodomys microps.* At the upper 2 stations the other rodents captured were all leaf eating species and would not be likely food competitors for deer mice. These species included *Microtus montanus, M. longicaudus,* and *Lagurus curtatus.*

DISCUSSION

Reproduction

It has been shown that there are definite altitudinal trends in the reproduction of *Peromyscus maniculatus* on White Mountain. These findings have been based on direct reproductive evidence and indirect evidence from population structure. The two criteria have complemented each other; in every case reproductive differences were born out by expected population structures. Table IX summarizes the findings, with the degree of each variable expressed numerically. Thus the population with the longest breeding season, greatest litter size, and most young produced is assigned the number 1; the population with the next highest potential is assigned the number 2, and so on. A gradient is observed in the increase of litter size (based on healthy embryos) and life expectancy with altitude. Length of breeding season and post-implantation mortality decrease with altitude. Apparently the total breeding season more than compensates for a smaller litter size at the lower elevation, for the number of young annually produced per adult female at 4,500 feet and 7,100 feet far exceeds that for the upper 2 stations.

TABLE IX. Altitudinal trends in reproduction. Numbers indicate relative increase (from 1 to 4) for each factor

elevation	litter size	life expectancy	length of breeding season	post-implantation mortality	young produced per female/year
12,400′.....	1	1	3	3	4
9,800′.....	2	2	2	2	3
7,100′.....	3	3	1?	1	2
4,500′.....	*	3	1?	*	1

*Not included as sample is too small (N=2).

It was expected that the breeding season at the higher elevations would be shorter because of the long cold winters experienced there. Breeding season data from the 12,400 foot station indicated that females average fewer than 2 litters each year. Females living at the 2 lowest elevations, with an aggregate breeding season of more than 6 months, are potentially capable of producing many litters in a year. Age structures for these lower populations reveal that this potential is at least partly realized.

The small number of pregnant females captured precludes any conclusive statement of altitudinal gradient in potential litter size; nevertheless, there was an apparent trend of increase in litter size with altitude. At the same time, post-implantation mortality (resorption) was commonest

(20%) at the 7,100 foot station and rare (2.6%) at the highest area. Trapping success indicated that the year-round deer mouse population was highest at 7,100 feet; furthermore, other seed eating rodents were found to be most abundant at this elevation. It would not seem to be mere coincidence that observed intrauterine mortality was also greatest for this area and least where the population density was lowest. Physiological stress is thought to be proportional to population density in some wild animals, and stress is known to have an effect on reproductive success (Christian 1956). Stress resulting from both interspecific and intraspecific strife may well be an important factor in reproduction in the White Mountain deer mice.

Mortality

Even with a relatively larger litter size, far fewer young are produced per female each year at the upper areas. Therefore, juvenile and adult mortality must be much less than at lower elevations. For example, it was calculated that 12% of the post-weaning mice at the 12,400 foot station live at least 2 years, while only 1% of the mice reach that age at 4,500 feet. Earlier studies have demonstrated that *Peromyscus* mortality may be lowest during winter months in some localities (Howard 1949). In the laboratory, *Peromyscus* can survive fairly low temperatures as long as food is available (Eskridge and Udall 1955), and thermometers placed in rodent burrows beneath the snow at White Mountain indicated that temperatures of the burrows seldom descended much below freezing, even when corresponding air temperatures were below 0°F. It is doubtful that the direct factor of cold winter weather has much detrimental effect on the deer mouse population at White Mountain. In fact, the heavy winter snow pack above 10,000 feet may reduce over-all mortality for the mice. Summer food caches are probably utilized in winter by mice living above snow line, and predator mortality, at least, would certainly be minimal whenever the mice remained beneath the snow.

Altitude as a factor of environment

Altitude, in its general sense, clearly has a measurable effect on the reproduction of deer mice. It is difficult, however, to separate the effects of low oxygen pressure from all other factors contingent upon altitude in wild populations. In laboratory experiments where all influences other than oxygen tension are kept uniform, low pressures may cause diminished reproduction (*e.g.* Moore and Price 1948), but these experiments have always involved a sudden change in physiological altitude, and so the conclusions are inappropriate to apply to populations in the wild. It seems probable that some of the altitudinal variation observed on White Mountain, such as differences in litter size, have a genetic basis, and that other phenomena such as differences in breeding season depend more upon contingent factors than upon altitude *per se* (*e.g.,* oxygen tension). Climate may well be the most important controlling factor.

SUMMARY

The reproduction of 4 wild populations of *Peromyscus maniculatus* living at 4,500, 7,100, 9,800, and 12,400 feet elevation on White Mountain, California, was studied over the year from October, 1956, through July, 1957.

Populations at the lower elevations were characterized by 2 main breeding seasons, in fall and spring, with sporadic breeding during winter and an aestival dropoff; mice at 9,800 feet bred during spring and summer with some winter reproduction; while mice at the highest altitude reproduced mainly in late summer and early fall. The aggregate breeding season in a year decreases with altitude at White Mountain.

A slight increase in mean litter size with altitude was observed, but this was more than compensated by the apparent production of more litters per year at the lower elevations. Population age structure, determined by a tooth-wear method, indicated that more than 3 times the number of young were produced per adult female at 4,500 feet than at 12,400 feet. Conversely, annual survival rates and life expectancy increased remarkably with higher altitude.

The aggregate sex ratio was 332 males to 227 females (40% females) and did not vary significantly with area or with age. Population density was greatest at 7,100 feet and least at the elevational extremes. Intrauterine mortality (reflected in resorption) was inversely proportional to the observed population density.

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INFLUENCE OF LIGHT ON MATING OF *DROSOPHILA MELANOGASTER*[1]

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Studies by Rendel (1951) indicate that illumination may influence mating in ebony and light forms of *Drosophila melanogaster*. Using the multiple choice method, Rendel found that ebony males mated only 48% as frequently as non-ebony (vestigial) in light, while in darkness the ebony males mated slightly more frequently than the non-ebony.

It appeared to the author that direct observations on melanistic forms of *melanogaster* might reveal interesting facts about the interactions of the flies as well as differential behavior under differing conditions of illumination. The present study was undertaken to obtain evidence on the questions: (1) Are ebony forms present in wild populations? (2) If so, do these forms show sexual isolation from light forms on the basis of mating behavior? (3) Is the behavior of ebony and light forms differentially affected by illumination?

Source of the Flies Used

Since it was desired to collect flies at a place remote from a *Drosophila* laboratory, collections were made at Beaufort, North Carolina on July 28, 1955. From a grocery garbage can 655 wild *melanogaster* were collected. Of these, 49 females and 58 males were slightly dark, having dark tridents and slight darkening of the sclerites in general, while 287 females and 261 males appeared light tan with little or no darkening of the trident. Females were isolated in vials of medium, and from these an attempt was made to separate 14 light and 14 dark strains by sib pair matings. In one of the cultures being selected for light, very dark flies (designated ebony) oc-

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casionally appeared. Attempts to isolate an ebony strain from these at first failed because the pairs did not breed. Meanwhile, in the light strain vial, ebony flies appeared continually. Finally, large numbers of these ebony flies were cultured in half pint bottles with banana medium, whereupon breeding began, although numerous non-hatching eggs were laid. (It was later found that crosses of ebony females and light males were highly prolific even on regular medium, while the reciprocal cross gave no yield on regular medium and slight yields on banana medium.) After about 15 months of culture, the ebony flies began to breed better and were then cultured with ease, even on regular medium. At this time an ebony and a light strain were made isogenic for chromosomes 1, 2, and 3 by means of a dominant inversion marker stock (j90) from Dr. H. J. Muller and a C1B stock from Dr. M. Whittinghill. The following studies were made mostly with these isogenic stocks, but the results were repeated in essence with non-isogenic (mass cultured) light and ebony stocks.

The ebony gene shows partial expression in heterozygotes, for when flies are cultured at 25°C some hybrids between light and ebony flies show intermediacy for the ebony condition, while others resemble the light parent. At 15°C, the ebony gene shows even greater expression in heterozygotes, the hybrids always being intermediate between the light and ebony parents. Ebony flies crossed with the laboratory mutant ebony$_{11}$ (from Dr. H. J. Muller) yielded all ebony flies in subcultures.

METHODS

The culture medium used was a modification of the Carpenter-Baker formula containing: 1000 cc water, 40g white ground cornmeal, 15 g agar, 40 g dried Fleischmann's yeast type 2019, 1 g KH_2PO_4, 8 g Rochelle salt, 100 cc white Karo syrup, 5 cc proprionic acid, and 0.5 g each of: NaCl, $CaCl_2$, $MnCl_2$, and $FeSO_4$. The medium was seeded with an aqueous suspension of dry active Fleischmann's yeast.

Flies were cultured by placing 50 female and 10 male adults in a half-pint milk bottle with about 50 cc of medium. Each day, the parents were transferred to a fresh bottle, and newly emerged flies, 10 females and 2 males, were added. The earlier flies emerging from these bottles were used for study.

Observation cells were made from 100 x 10 mm petri dish bottoms containing medium. A piece of cellophane with 100 holes made with a dissecting needle was fastened on top of the dish with a rubber band. These cells were placed in 2 round cardboard containers 150 mm in diameter and 25 mm high. One container was covered with clear cellophane, and on the other was taped a clear round plastic dish 150 mm in diameter and 25 mm high containing an aqueous solution of neutral red sufficiently concentrated so the flies beneath were just visible and would not move suddenly when a 150 watt desk lamp, about a foot above the cell, was turned on. This cell is referred to as the diminished light cell. Air was admitted to the 2 containers through rubber tubes coming from a bottle into which air entered from a jet. Both containers were kept under constant illumination from overhead flourescent lights in the air conditioned laboratory (22°). A Weston Photoelectric Light Meter with quartz filter showed a reading of 66.20 f. c. when placed beside the cells.

Flies were collected and etherized within an hour after emergence from the pupal cases in the culture bottles. Forty flies of each sex and body color (light and ebony) were placed in each 35 X 100 mm vial with medium and kept at 25°C in the dark for 4 days. The flies were then re-etherized and 15 of each sex and body color were placed in the full light and diminished light cells. They were then constantly observed with a magnifying glass for 5 hours (after which matings were very infrequent). The positions of mating flies were marked on diagrams of the observation cells, and the mating times were recorded. A desk lamp was sometimes turned on momentarily to determine the phenotypes of the mating flies in the diminished light cell. In all, 28 runs were made on a total of 420 flies of each body color and sex.

Since it was desired to supplement the observation cell studies in a large enclosure in which the flies had more freedom and could depart from the food dishes, a 854 X 325 X 303 mm aquarium was covered with a glass lid. The floor of the aquarium was padded with moist toweling on which 100 X 10 mm petri dish bottoms with medium were placed. Some flies placed in the aquarium were individually marked with dots of aluminum paint placed on top of the thorax with the point of an insect pin. The aquarium was placed on the table near the observation cells, and activity related to territorial behavior was studied.

BEHAVIOR

It was early noted that when the observation cells were unequally illuminated, light flies aggregated toward the lighted side much more than did ebony flies. When the cells were kept in diminished light, such aggregation was not shown.

The courting and mating of light flies is similar to that described for the species by Spieth (1952). Ebony flies, however, show many deviations from this pattern. Ebony males are obviously less quick in posturing and circling than are light males and these preliminaries are usually omitted. Instead, they immediately lick the wings and body of the courted fly while bending the tip of the abdomen and making thrusts. Ebony males sometimes extend their wings during courtship, but the extension appears slow and is often directed away from the head of the courted fly, while light flies almost always extend the wing toward the head. Ebony males sometimes made copulatory motions toward each other's heads, and in 7 such cases one male clasped the other's proboscis with his abdominal claspers. The victim did much kicking and struggling while the clasping male remained passive. One of these pairs was killed with CCl_4, and microscopic examination showed the left part of the labellum of the proboscis of one male under the left abdominal clasper of the other. This male-by-male clasping was not observed among light flies. Females seem more easily able to elude ebony than light males. Light males readily push aside and replace courting ebony males.

Ebony females move away from courting males less quickly than do light females of the same age. When a male succeeds in mating with her, an ebony female does not usually stand quietly while the male settles between her wings as do light females, but she bends down the tip of her abdomen and kicks and struggles and sometimes spins and tumbles about until finally becoming more quiet and kicking only occasionally. Throughout mating, the male typically remains at an angle of 90° or more from an ebony female's abdomen rather than settled upon it with his legs clasping the female's wings as is the case with light females.

Light males, even when newly emerged or decapitated, are active in wing flicking, which is usually followed by apparent mutual toleration of males rather than elimination of males from the scene of activity. Ebony males flick their wings less frequently and less quickly, but fight more than do light males. This fighting consists of "charging" *i.e.* making a sudden dash at another male, with or without countercharging on the part of the other male. The abdomen is sometimes intermittently flexed during charging. Before charging, light males, much more than ebony males, extend the wings, usually simultaneously, about 45° up and back. The wings may be held in this position for as long as 15 seconds during which time the male charges other males particularly readily. In actual charging, these males extend the wings forward to about 90°. The wings are finally folded either simultaneously or one a little later than the other.

Charging frequently leads to "tussling," sometimes very vigorous, in which a charging male may pounce on the other from any angle and tug the wings and body of the other male while flexing his abdomen. These tussles may become mutual, whereupon males face and tug at each other and push and sometimes tumble about as in wrestling. Although bouts of tussling and charging (as observed among individually marked flies in the aquarium) are usually only one to 2 seconds in duration, they may last intermittently up to at least 115 seconds. Sometimes 3 males are involved in the same tussel. After such fighting, one of the males may depart flicking his wings. He may return, in which case the activity may be resumed, or the departure may be lasting. A charged male may leave quickly without return charge. Many males may fight with, and subsequently depart from, the same male on a dish. On one occasion 8 males were observed to depart from one charging male within 2 minutes.

Ebony males fled much more readily from charging males than did light males. Light males often remained standing and flicking their wings when charged, in which case the charging male would usually desist. No males were observed fighting prior to 24 hours after emerging. The frequency of fighting increased as the flies aged. Females were never observed to tussle, but they sometimes briefly charged other flies standing in their paths as they were feeding. In the aquarium, fighting was observed only on the food dishes although, of 226 observed matings, 73 occurred off of the dishes.

In the 5-hour periods of observation of light and ebony flies in the observation cells in full light (Table I) ebony males mated with 88 ebony females but with only 13 light females. Under the same conditions, light males mated with 137 ebony and 131 light females. It seemed, thus, that in the light, ebony males mated preferentially with ebony females, while light males mated at random. Within an equal interval in diminished light, ebony males mated with 132 ebony females and only 47 light females. Similarly, light males mated with 129 ebony and 93 light females. It thus seemed that in diminished light, both ebony and light males mated preferentially with ebony females.

The mean interval between entry and mating

TABLE I. Total matings and mean hourly intervals between entry and mating of virgin flies aged 4 days before entry into observation cells in light and diminished light

Mating System (Males on Left)	Hourly Interval Between Entry and Mating in Light (Mean ± S.E.)	Total Matings in Light	Hourly Interval Between Entry and Mating in Diminished Light (Mean ± S.E.)	Total Matings in Diminished Light
Ebony x Ebony	4.20±0.35	88	2.82±0.29	132
Ebony x Light	4.45±0.75	13	4.00±0.26	47
Light x Ebony	1.58±0.07	137	2.86±0.21	129
Light x Light	1.64±0.05	131	2.95±0.42	93
Ebony Males	4.27±0.31	101	2.96±0.03	179
Light Males	1.61±0.06	268	2.90±0.01	222
Ebony Females	2.31±0.01	225	2.85±0.17	261
Light Females	1.97±0.13	144	3.08±0.38	140

of ebony males was 4.27 ± 0.31 hours in the light and 2.96 ± 0.03 hours in diminished light, indicating that ebony males mated earlier in diminished light. The mean interval between entry and mating of light males was 1.61 ± 0.06 hours in the light and 2.90 ± 0.01 hours in diminished light, indicating, in contrast to ebony males, a much earlier mating in the light cells.

It appeared that ebony males were mating preferentially with ebony females under both lighting conditions. Light males appeared to do similarly in diminished light, but in full light they mated at random. In an attempt to determine whether it is the males that are active in selection rather than the females, the heads and wings were removed from 30 light and 30 ebony females, which had been aged 4 days as virgins. The headless and wingless bodies were randomly mixed in an observation cell with 50 etherized males, aged 4 days without females. (Removal of heads prevented the females from escaping from the males, and removal of wings prevented the females from flicking toward males. The females could still stand and push the males with their legs, but this behavior was not a serious impediment to the study.) The cell was observed in full light and for an equal amount of time in diminished light. Two parallel wires stuck in a cork were drawn slowly across the cell, and the number of times males were observed extending their wings toward females between the wires was recorded. If a male persisted in extending his wings toward a female, his activity was recorded each time the wires passed over him. After 7 cells had been made up and observed using light males, 7 were set up and similarly treated using ebony males.

Ebony males extended their wings about as often toward ebony as toward light females (Table II). In the light, they extended their wings 326 times toward ebony and 316 times toward light females, and in diminished light, 794 times toward ebony and 786 times toward light females. Light males, on the other hand, extended their wings mostly toward light females in the full light, where they extended 943 times toward light females, but only 662 times toward ebony females. In diminished light, they showed little, if any, preference and extended 312 times toward ebony and 292 times toward light females.

TABLE II. Wing extensions and matings of light and ebony males toward headless and wingless light and ebony females in light and diminished light

Type of Interaction (males on left)	Wing Extensions in Light	Wing Extensions in Diminished Light	Matings in Light	Matings in Diminished Light
Ebony x Ebony	326	794	4	2
Ebony x Light	316	786	1	3
Light x Ebony	662	312	1	1
Light x Light	943	292	6	1

There was an insignificant number of matings with the headless and wingless females. Three of these were with the same female. Some males appeared to become stuck while mating with these females, and one of them caused extension of the female's vaginal plates while pulling away after mating.

To determine whether crowding of males interfered with mating, 2 cells were set up in full light with 30 of the light 4-day virgin females in each. To one cell were added 30 of the 4-day light males, and to the other, 150 similar males. Five runs were made.

A count showed 122 matings in the cells with 30 males and 58 matings in the cells with 150 males. The lower number of matings in the cells crowded with males appeared to be due to interference with courtship, and to mass chases of females.

SEX RECOGNITION

Males seemed readily able to recognize sex, for they sometimes tussled with numerous other males in rapid succession, then, upon coming to a female, they would begin courting. Some males courted copulating females from the front, then later charged the copulating male from the rear. It appeared that something other than behavior was involved in sex recognition.

In early tests to determine whether odor played a role in sex recognition, ebony flies about 8 hours after emergence were used. Spots of aluminum paint were placed on the thoraces of 100 males, and juice forced from the tips of female abdomens was also placed on the males. A spot of aluminum paint was similarly placed on the scutellum of each of 100 similar males on which juice forced from the tips of male abdomens was placed. The males were re-etherized and placed in an observation cell in full light with 30 ebony males which had been aged 4 days without females. Of these 4-day males, 155 were observed making precopulatory motions toward female-treated males, while only 41 were observed making such motions toward male-treated males.

The agar on the bottom of an observation cell was then marked into 8 equal sectors. In each sector, 10 heads from light flies were arranged equidistantly in a triangle with rows of 4, 3, 2, and one, the 4 row being peripheral. In one sector were heads of day-old males, in the next, heads of freshly-emerged females, and in the remaining 6 sectors, heads from females aged 1, 2, 3, 4, 5, and 6 days. Then 30 light 4-day males were introduced and the numbers of wing extensions made toward the heads were recorded. Each sector was observed for an equal amount of time in a rotating system. Males persisted in wing extension in a sector were recorded once each time that sector was observed. The cell was then placed in diminished light and observed for an equal time. A total of 5 such cells were used.

TABLE III. Wing extensions of males toward heads of flies of various ages

Age of Head Donors (in days)	Sex	Wing Extensions in Light	Wing Extensions in Diminished Light
1	m	26	0
0	f	70	67
1	f	321	201
2	f	117	126
3	f	84	85
4	f	84	68
5	f	51	66
6	f	79	73

In diminished light (Table III) no wing extensions toward male heads were observed. In full light, fewer extensions were made toward male than toward female heads. More extensions were made toward 1-day and 2-day female heads than toward the others.

This raised the question as to whether males would mate more readily with young than with old females. Two cells were set up in full light. In each cell 30 light 4-day males were placed. In one cell were placed 30 light 2-day virgin females marked with a spot of aluminum paint on top of the thorax and 30 light 6-day virgin females marked on the scutellum. In the other cell were placed similarly-marked ebony females aged 2 and 6 days. Seven runs were made and matings were counted for 5 hours as usual.

Among light females, the older ones mated in greater numbers (77) than the younger ones (39). But among ebony females the older ones mated in about the same number (71) as the younger ones (68).

DISCUSSION

The charges and tussles of the male *Drosophila* appear to be forms of aggression. Since the behavior is followed by the elimination of males from the areas where the behavior is staged, such activity may be described as territorial (though of a brief transitory sort) provided that the definition of Noble (1939) of territory as "any defended areas" is followed.

The lack of marked territorial behavior of long duration in *Drosophila* may be correlated with the ability of females to repel males by extruding (cf. Spieth 1952). This may prevent molestation of ovipositing females just as marked territorial behavior appears to do in Odonata (Jacobs 1955). The same problem of extra-male interference with ovipositing females could be solved by adjusting the sex ratio so that fewer males are present. But the excess males, by interfering with mating and oviposition on attractive, but limited, food sources may actually aid the species by forcing females to fly to less attractive, but in the long run more favorable, places, thereby preventing excessive concentrations of larvae and aiding dispersal. It may be that there is an optimal balance between interference and non-interference with ovipositing females under different conditions of population density.

Wing flicking probably should not be considered aggressive, for it appeared to be followed by mutual toleration rather than by elimination of males from the scene of activity. It is interesting that wing flicking was observed among newly emerged males, but fighting was observed only among males at least about a day old by which time mating was occurring. Perhaps wing flicking is less directly related to mating than is fighting.

The failure of ebony males to circle and posture at a distance from the courted flies, and the tendency of such males immediately to begin licking the courted flies, would seem to indicate that ebony males employ less vision in courting than do light males. This behavior, in connection with negative phototaxis (as indicated by failure of ebony flies to aggregate as much as light flies toward the lighted side of observation cells) would seem appropriate for inhabiting dark places such as cavities. Although ebony, being apparently rare in nature, may not itself be an adaptive type, the behavior of ebony flies possibly reflects similar behavior in other dark flies which are common in nature. *Drosophila melanica,* for example, occurs as a dark form in eastern woodlands and as a light form in western deserts of the United States (Ward 1952). An ecological study of these forms should be interesting.

The habit of ebony females of bending down their abdomens and kicking while mating may be an avoidance reaction. Wallace and Dobzhansky (1947) and Spieth and Hsu (1950) have described similar behavior in interspecies *Drosophila* crosses. Perhaps ebony females are not well equipped to prevent copulation. They are markedly slower at eluding courting males than are light females, and this may lead to ill-adjusted copulation. This may explain why ebony females mate earlier than light females.

The hypothesis that light females differ from ebony females in their resistance to males is supported by the facts that older light females, mate more readily than younger ones while old and young ebony females mate about equally readily. Perhaps aging of light females lowers their resistance to courting males, while ebony females do not have as much resistance which is amenable to lowering.

The studies indicate that odor may play a role in recognition, for, in diminished light, males did not court male heads but did court female heads, especially young ones. Several authors have suggested that odor may play a role in courtship. Sturtevant (1915) found that flies placed in vials in which copulation had just occurred were more likely to mate than flies placed in clean vials. (Since this seemed hard to believe, the writer repeated these studies and got results similar to Sturtevant's). Spieth (1949) suggested that chemoreception is probably responsible for the failure of mating between *D. willistoni* females and *D. capricorni* males, which often break off courtship without having come into direct contact with the females. Miller (1950) made similar suggestions in his studies of *D. affinis* and *algonquin*.

SUMMARY

Light and ebony forms of *Drosophila melanogaster* were isolated from a grocery garbage can at Beaufort, North Carolina. Isogenic and non-isogenic cultures of these flies were studied by direct observation in petri dish cells in full light and diminished light and in an aquarium in the light.

1. Ebony males usually failed to posture and circle courted flies at a distance, but made immediate contact, licked, and made abdominal thrusts toward the courted fly. Ebony males made more wing extensions away from the head of courted flies than did light males. Mutual head-on courtship of ebony males sometimes led to one clasping the proboscis of the other with his abdominal claspers. Light males readily displaced courting ebony males.

2. Ebony females moved away from courting males markedly less readily than did light females. Teneral ebony females almost invariably tended to bend down the tip of the abdomen and kick and struggle while mating.

3. On the food dishes, males charged and tussled with other males, after which departures sometimes occurred. Certain males thereby dominated others. Light males readily dominated ebony males.

4. In observation cells, a greater percentage of ebony flies mated in diminished light than in full light, while light flies did the opposite. Under both conditions, ebony males mated with ebony females more frequently than with light females; light males did similarly in diminished light, but in full light they mated with ebony and light females about equally.

5. With headless and wingless females, light males extended the wings in courtship more toward light than toward ebony females in the light, while ebony males in full light, and both types of males in diminished light, extended toward light and ebony females about equally. Ebony males courted more in diminished light than in full light, while light males did the opposite.

6. Crowded males interfered with each other's courtship and made mass chases toward females, resulting in fewer matings in cells where males were crowded.

7. Males courted males on which the juice of females had been placed more than those on which male juice had been placed. In the light, males courted the heads of females more than the heads of males; they did not court male heads in diminished light. Males courted heads of 1-day or 2-day females more than those of older or teneral females. Males mated oftener with old (6-day) than with young (2-day) virgin light females but, with ebony females, this difference was not noted. The relation of this to readiness to mate and subsequent avoidance behavior of ebony females is discussed.

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A FEEDBACK MECHANISM OF GROWTH CONTROL IN TADPOLES[1]

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INTRODUCTION

Many observations in the field and in the laboratory have established the relationship that growth rates of aquatic organisms may depend upon their numbers and, up to a limit, the size of the container in which they are growing. Pertinent references are cited in the Discussion. Although the "Lebensraum" or crowding phenomenon is a well recognized biological problem, no explanation of it has as yet withstood critical scrutiny. Experimental evidence presented here plus the recent work of Richards (1958) give reasons for believing that tadpole growth is limited in feedback fashion by rather specific products of their metabolism or growth.

CULTURE PROCEDURES

At the outset it was apparent that the quality of culture water greatly influences tadpole growth. The standard laboratory water had been dechlorinated by passage through charcoal filter beds. This water is still toxic to tadpoles, probably because of the addition by the water company of copper sulfate in concentrations which may run as high as 0.8 of a part of copper per million. To chelate the copper, versene was added (50 mg per liter) as suggested by Loomis and Lenhoff (1956) for the culture of *Hydra*. Before addition of the versene tadpoles receiving new dechlorinated water daily failed to grow for more than 2 or 3 weeks. After daily change of dechlorinated and versenated water became routine practice, growth proceeded normally from early tadpole stages through to metamorphosis.

In addition much of the water used in the experiments was previously heterotypically conditioned by serving as the culture medium for a variety of organisms not including tadpoles. The practice is to start with dechlorinated and versenated city water. This is kept in 15 liter or larger aquaria containing a variety of aquatic plants, snails, tropical fish and a complex microflora and microfauna. The aquaria are lighted by 40 or 60 watt bulbs at a distance of 10 cm for from 10 to 16 hours per day. Every day approximately one-third of the water is removed for use in tadpole experiments. The water removed from the conditioning aquaria is replaced by dechlorinated and versenated water. Such water with one-third changed daily will support greater growth of uncrowded tadpoles in 70 liter aquaria than is found in many ponds.

The food used is Purina Rabbit Chow. It is a pressed, partially dehydrated combination of plant parts furnished in the form of pellets. In addition the tadpoles receive small amounts of microflora and microfauna in the water from the conditioning aquaria. The advantage of such a food is that the tadpoles can be fed maximally

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[1] This work was supported by grants from the National Science Foundation.

without fouling the water. More food than the assay tadpoles will eat is added at the time of daily water change. One learns by practice how much tadpoles of different sizes will eat, and that those in large containers require more food than those in small containers.

In most of the experiments *Rana pipiens* tadpoles were used. They were grown from eggs after ovulation had been induced by injections of pituitary glands (Rugh 1934b). The *Rana catesbiana* were collected as eggs from a pond near Woods Hole, Massachusetts.

Growth in Small Containers

This work began with the practical question of how many recently hatched *Rana pipiens* tadpoles could be cultured through to metamorphosis in fingerbowls of 18 cm diameter containing one liter of water changed daily. One tadpole alone in a liter grows rapidly and metamorphoses. Two are slower but they can both metamorphose and become healthy frogs. Four in one bowl grow more slowly and usually all 4 can metamorphose, but 2 or 3 of these are stunted and metamorphose long after the first has metamorphosed and been removed from the bowl. If more than 4 are grown in a liter most are stunted and seldom do more than 3 or 4 of them metamorphose successfully.

The tadpoles were weighed periodically, and from the weights some unexpected relationships emerge (Table I). Total weight increases with number of tadpoles. The more tadpoles one begins with per liter, within the limits of the numbers of this experiment, the more the total weight of tadpoles achieved. In experiments by Lynn and Edelmann (1936) the same relationship was obtained except that in their most crowded compartment so many tadpoles died that the final weight was decreased.

A single tadpole in one liter of water may achieve a weight of 5 g before it absorbs its tail. When more are present the largest seldom achieves a weight of 3 g, and the average was in all cases under 3 g.

Although the container under these space-limited conditions may be said to limit growth, the relationship obtained is not that the container or the water in it will support only a certain amount of tadpole growth. It might seem so if only the growth of one and 2 were compared. Two tadpoles stop growing with each weighing about 2.5 g, only about half the weight of one alone. However, a one liter container will support the production of much more than 5 g of tadpole—about 50 g when 40 are present and 67 g when 66 are grown together.

Table I. Maximum weights attained by tadpoles in one liter of water

Number of Tadpoles	Total Weight	Average Weight	Weight of Largest	Weight of Smallest
1	5.3	5.3	5.3	5.3
1	5.1	5.1	5.1	5.1
1	4.9	4.9	4.9	4.9
2	5.1	2.6	3.1	2.0
2	5.0	2.5	2.7	2.3
3	8.6	2.9	3.0	2.6
3	7.6	2.5	3.6	1.3
3	6.0	2.0	2.1	1.9
3	5.8	1.9	2.4	1.7
4	8.5	2.1	2.9	1.5
4	7.3	1.8	2.8	1.3
4	6.5	1.6	2.0	1.2
5	7.2	1.4	1.9	0.5
5	9.5	1.9	2.2	1.7
6	6.9	1.2	1.8	0.6
7	9.4	1.3	2.3	0.8
39	55.6	1.4	2.3	0.3
39	45.6	1.2	2.2	0.3
40	49.9	1.2	2.2	0.2
66	67.1	1.0	2.3	0.2

Very few of 66 can be expected to metamorphose successfully. The average weight is one gram and this is too little for *R. pipiens* at the the time of metamorphosis. Few below 2 g at the time of metamorphosis are capable of growing after metamorphosis. There is also an appreciable number of deaths when tadpoles are crowded this much. In this experiment the number at the beginning was 85. Nineteen had died before the maximum weight of the group had been reached. The 19 died over a period of weeks. During the same period some of their siblings in the same container were growing quite rapidly.

Whenever more than 8 tadpoles are grown in a liter of water it is almost certain that some will die before metamorphosis. In this experiment 19 of 85 and 10 of 50 had died. After the tadpoles, all about the same size originally, had been living together for 10 days, appreciable size differences were noted. Growth rates were so varied that weights at the end of the experiment ranged from 2.3 g for the largest of 66 down to 0.2 g for the smallest. What one observes when the concentration is great enough to cause some to die, is that after a time the smallest individuals fail to take food even when it is plentiful. Before that there is often a period of approximately 2 weeks when they eat just enough to maintain their weight. After that they take less and become narrow in the abdominal region. However, at any time before there is actual loss of weight these much stunted tadpoles may be isolated in the same kind of water and with the same kind of food, and they will grow. They have simply been removed from their larger siblings. This means that their fellows had been inhibiting them in some way.

Another relationship is apparent in Table I. One tadpole growing alone in a liter of water is appreciably larger than any of those growing in groups as noted above. The new relationship is that the largest tadpoles in groups, from 2 to 66, all weigh about the same, somewhere between 2 and 3 grams. The largest have achieved at the time of metamorphosis roughly the same weight whether they have one or 65 bowlmates. The smallest, even the average under the more crowded conditions, are badly stunted. Still, there is usually one per bowl that grows as though there were only one other with it no matter how many there really are. Could it be that once a sufficient size difference has been attained the larger inhibit the smaller, but that the smaller do not inhibit the larger? This is one of the questions to be answered.

So far we know from the studies in one liter containers that total growth increment increases as the number of individuals is increased. At the same time the average mass of the individual tadpole decreases. Going beyond the average we see that the largest grow at about the same rate no matter what the concentration between 2 and 66.

At this point we know that some tadpoles inhibit their fellows. Since an excess of food was present, we know that the inhibition was not exercised through preemption of food. Several questions arise. Are the larger tadpoles inhibitory because they are larger? Is the inhibition a result of the more rapid removal of some trace substances by the growing tadpoles? Is it by the addition of inhibitory materials by the growing tadpoles? Could it be that the larger tadpoles have a psychological effect on their smaller fellows which reduces feeding? Are the tadpoles inhibited by collisions? These are questions which will be answered below, but we must first consider growth relationships in larger containers.

Growth in Larger Containers

The same general relationships are apparent whether tadpoles are cultured in one liter or 12 liter containers. As would be expected from past work (Yung, 1885, de Varigny 1894, Bilski 1921, Goetsch 1924, Rugh 1934a), the average weights increased as the container size was increased (cf. Table I and Table II), but here again we find an unexpected relationship.

R. pipiens tadpoles were cultured in aquaria containing 12 liters of water with a water depth of 16.8 cm and length and width of 36 and 20 cm. As the number of tadpoles was increased from 14 to 53 the average maximum weight decreased from 5.1 g to 4.2 g. However, and this is the unexpected relationship, the maximum weight of the largest 14 was the same whether there were 14, 16, 37 or 53 living together. The 14 alone weighed 71.3 g or an average of 5.1 g. The 14 largest of 16, the 14 largest of 37 and even the 14 largest of 53 also averaged 5.1 g (Table II).

Table II. Maximum weights (grams) attained by tadpoles in 12 liters of water

Number of Tadpoles	Total Weight	Average Weight	Total Weight Largest 14	Average Weigth Largest 14
14..........	71.3	5.1	71.3	5.1
16..........	79.9	5.0	71.4	5.1
37..........	171.8	4.6	70.9	5.1
53..........	222.7	4.2	71.8	5.1

We see even more strikingly than in the one liter bowls that, given a certain size container, the arbitrarily chosen number of largest tadpoles achieves the same size in all containers.

Could it be that the larger members of a group develop without appreciable influence from their smaller neighbors? The smaller, on the other hand, seem to be greatly affected by their larger aquarium mates. When the group of 53 had reached its maximum weight the largest 14 averaged 5.1 g and the total group averaged 4.2 g, but the smallest 5 averaged 0.35 g. Other small ones had already died. Just as in one liter bowls the smallest individuals had finally stopped eating and had died. The original number had been 75. Twenty-two had died leaving 53 alive.

Here, too, an excess of non-fouling food had been supplied. Water had been changed every few days during the first half of the experiment, and every day during the second half. Some tadpoles had grown well while others grew more slowly at first, stopped growing and died. A direct experiment to test whether larger tadpoles inhibit growth of smaller ones was indicated.

Effect of Large on Small

Five aquaria each containing 8 liters of heterotypically conditioned water and plants of the genera, *Anacharis, Fontinalis* and *Hygrophila* and several small platy fish, *Xiphophorus maculatus* were lighted for 15 hours per day and maintained at 26°C. Half of the water was replaced daily. With these conditions tadpoles grow very rapidly. Six tadpoles weighing 0.1 g apiece were placed in each of the 5 aquaria. Three of the aquaria received in addition a single larger tadpole weighing 2.5 g at the beginning of the experiment.

In the 2 aquaria where 6 small tadpoles were cultured without a larger tadpole there was a 4- to 5-fold increase in weight during the 2 week test period. At the same time the 3 sets of small tadpoles failed to grow or lost weight slightly while their single inhibitor grew rapidly from 2.5 g to more than 5 g and began to metamorphose (Table III).

TABLE III. Growth of small tadpoles with and without a large growing tadpole

	Total weight of 6 assay tadpoles at start	Total weight of 6 assay tadpoles 14 days later
With larger tadpole (growing from 2.5g. to 5+ g.)	0.6	0.6
	0.6	0.5
	0.6	0.4
Without larger tadpole	0.6	2.8
	0.6	3.0

In this experiment conditions were arranged so that small tadpoles and large tadpoles could grow very rapidly, but when they were combined the small failed to grow.

It was thought that there might be great mutual inhibition if tadpoles were confined in a very small volume of water. Fingerbowls, 10 cm in diameter and containing one quarter liter of water, changed daily, support slow growth of single *R. pipiens* tadpoles up to 0.7 g. Growth stops at this weight. Legs, which grow most toward the end of the tadpole stage, are disproportionately small when metamorphosis begins. Never, out of more than 100 cases, have we been able to have a tadpole grown in one quarter liter of water complete metamorphosis.

One, two or four 0.1 g tadpoles were started in small finger-bowls containing one quarter liter of water, not enough to allow metamorphosis of even one. This experiment has been performed 3 times, always with the same results. The results of one experiment done in triplicate are recorded in Table IV.

Single tadpoles typically grew better than those in groups. As seen earlier in one liter and 12 liter containers, the largest in the groups achieved approximately the same weight independently of their number. There was appreciable stunting of some, especially in the groups of 4. However, in this confined space, too small for the completion of growth of even one, instead of inhibition being complete for some, all grew some. Furthermore, in the period from 25 to 37 days when weight differences of partners were as great as 5 times, there was in most instances appreciable growth of the smaller partners. Under these very poor growth conditions in small bowls inhibition was nowhere near as great as under good growth conditions in 32 times as much water (Table III). It appears that greater inhibition is associated with greater growth.

TABLE IV. Weights achieved in quarter liter containers. At start all weighed 0.1 g.

	Weight after 25 days	Weight after 37 days
Singles	.55	.90
	.50	.80
	.35	.50
Two together	.25	.45
	.20	.30
	.50	.45
	.10	.35
	.35	.35
	.15	.30
Four together	.30	.55
	.20	.25
	.15	.20
	.10	.20
	.30	.45
	.25	.30
	.15	.20
	.10	.15
	.25	.40
	.20	.25
	.20	.20
	.15	.15

In all experiments reported above care had been taken to have a little more food in the containers than the tadpoles could eat. Larger was not inhibiting smaller in a direct competition for food. The time has come to consider the possibility that a feedback system involving products of growth or products of metabolism was controlling growth rate.

INHIBITORY CULTURE WATER

If growing tadpoles are cultured in a liter of water and every day their culture water removed and assayed for its effect on growth of small tadpoles, it is learned that the growth of the assay tadpoles is greatly inhibited. This basic experiment has been repeated over 100 times, always with the same result. The number of tadpoles used to make a liter of water inhibitory in 24 hours has varied from one to 60. Richards (1958) has shown that time needed for large tadpoles to make water inhibitory is just a few minutes.

A decrease in growth rate of the assay tadpoles as compared to controls receiving heterotypically conditioned water is noted within 2 to 4 days if the assay tadpoles have entered the logarithmic portion of the growth curve. During this period of rapid growth any inhibition effected through their culture water is soon apparent. Routinely 4 assay tadpoles each weighing between 0.1 and 0.2 g receive culture water daily from other tadpoles.

As a first attempt to learn the nature of the inhibitory products, culture water in which tadpoles had lived for one day was heated to different temperatures and assayed for inhibition. Culture water from 10 to 20 tadpoles per liter was collected daily and pooled. One liter aliquots were assayed as above after having been heated to 40°, 60,° 85° or 95°, cooled and aerated. Part of the pooled culture water remained at 20°C and growth in it serves for comparison. This experiment was first done, in duplicate, by Esther Olle as part of a class experiment. It has been repeated 3 times by the author and in a slightly different way by Richards (1958).

The results of a typical experiment are plotted (Figure 1). Growth was relatively slow in unheated culture water. Growth was slightly better when the culture water was brought to 40°, immediately cooled and aerated before assay. After heating to 60°, 80° or 95°C the culture water promoted much better growth, as good as found in heterotypically conditioned water.

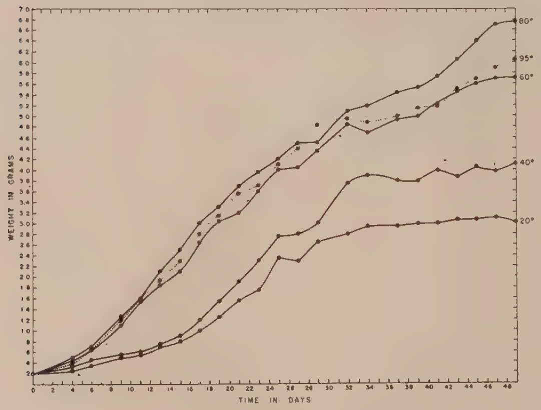

Fig. 1. Growth curves of assay tadpoles receiving culture water from larger tadpoles. The water had been heated to different degrees, cooled and aerated before use on 4 assay tadpoles in one-liter bowls. The water was replaced daily, and the tadpoles were fed maximally. Weights are totals for 4 assay tadpoles.

The slight difference between the 20° and 40° curves may or may not be significant. Approximately the same slight difference and in the same direction has been observed 5 out of 5 times. The differences in the range from 60° to 95° are not significant. In different replicates the 80° and 95° curves have been on top. In another experiment in which some of the culture water had been heated to 70° there was better growth in it than in water heated less or more. The indication is that culture water begins to lose its acquired inhibition when heated to 40° and that all of the inhibitory material has been lost by the time the temperature reaches 60° or 70°. The inhibitory material is quite stable at 20°. Appreciable inhibition is still exerted by culture water removed from tadpoles and allowed to stand for one week. After standing one month it is no longer inhibitory.

The nature of the inhibitory agent has been studied by Richards (1958). Her centrifugation and filtration studies indicated that inhibition was associated with large particles, larger than bacteria. Their possible cellular nature was indicated by the fact that sonication, ultra-violet irradiation, heating to 60°, or freezing and thawing—all treatments which destroy cells, also removed the inhibition. In addition, treatment by a variety of enzymes did not affect the inhibition, again indicating a possible cellular nature. The cells may be intestinal epithelial cells which are sloughed in great numbers, but this is not certain (Richards 1958).

INDICATIONS OF FEEDBACK CONTROL

That complete inhibition of small by large was obtained under excellent growth conditions, which seemed paradoxical at first, had suggested a feedback system. In addition it had been noted several times that tadpoles removed from large, well planted aquaria containing tropical fish and snails ceased growing when transferred to one liter culture bowls containing the usual heterotypically conditioned water. Furthermore, culture water from these non-growing tadpoles did not inhibit growth of assay tadpoles. Because this also suggested the possibility of a feedback with products of growth inhibiting growth, a comparison was made of the growth regulating properties of growing tadpoles and non-growing, starved tadpoles. Water was taken daily for assay from 1½ liter bowls containing 4 tadpoles weighing approximately 0.25 g apiece at the beginning of the experiment. Three groups of 4 were fed maximally. Another comparable 3 groups had no food added except the minor amount in solution and in suspension in the heterotypically condi-

TABLE V. The effect growth of culture water from fed and from starved tadpoles. Experiment done in triplicate. Figures are averages in grams for the 3 experiments

	FED 4 tadpoles in 1 ¼ L of heterotypically conditioned water, fresh daily. Fed maximally. Grew from 3.0 to 6.85 g.		STARVED 4 tadpoles in 1 ¼ L of heterotypically conditioned water, fresh daily. Starved. Lost weight from 3.0 to 2.85g.		CONTROLS	
	Every day water removed after 24 hours and separated into		Every day water removed after 24 hours and separated into		Received heterotypically conditioned water daily	
	1 L for 1 assay tadpole	¼ L for 1 assay tadpole	1 L for 1 assay tadpole	¼ L for 1 assay tadpole	1 L for 1 tadpole	¼ L for 1 tadpole
Weights at beginning.....	0.3	0.3	0.3	0.3	0.3	0.3
Weights at end of 14 days..	0.4	0.5	1.85	1.1	2.1	1.2
Increments..............	0.1	0.2	1.55	0.8	1.8	0.9

tioned water which they received daily. Water from the fed and starved groups was distributed daily to assay animals. In this experiment single tadpoles weighing initially 0.1 g served as assay animals. The reason for the change in method was that it had been learned that in addition to the effect of the culture water being assayed we were also getting an inhibitory effect of the assay animals on each other. This tended to mask the effect of the water being tested.

The results are clear. In 12 days while assay animals receiving water from starved tadpoles and controls receiving heterotypically conditioned water were increasing 6 and 7 fold in weight those receiving water from fed animals scarcely grew at all (Table V).

Assay animals receiving the same inhibitory culture water but living in one quarter liter bowls grow less rapidly than their siblings in one liter bowls (Table V). It appears that even with only one animal per bowl there is appreciable self-inhibition. This is not great enough, however, to obscure the strong inhibitory effect of water from feeding tadpoles. We are studying a feedback in the sense that growing tadpoles produce something which suppresses growth of tadpoles.

SPECIFICITY OF EFFECT

In work of this kind the question always arises, "Are the inhibitors general metabolic wastes?" If so, addition of quite unrelated organisms should reduce the growth rate of a given species. If, on the other hand, the inhibitors are more specific, only more closely related organisms should be mutually inhibitory. We are not concerned here with another class of substances, the antibiotics, which have their greater effect on distantly related forms.

The details of this phase of the work are to be reported in another publication. Only a summary of the experiments will be presented here.

R. pipiens tadpoles were grown in a range of concentrations such that the addition of more tadpoles would have caused an appreciable effect on the growth of the more stunted individuals. Their growth curves were compared with those of identical groups of tadpoles cultured with other organisms. In all cases, with one exception, it was found that partially inhibited *R. pipiens* tadpoles were not further inhibited by other organisms. The ones which did not inhibit further are the urodeles, *Notophthalmus* (= *Triturus*) *viridescens* and *Necturus granulosa,* the fish, *Xiphophorus maculata, Lebistes reticulatus* and *Tanichthys albonubes,* and the snail, *Physa.* The exception, and this inhibited appreciably, was a member of the same genus, *R. catesbiana.*

In all cases, with the single exception of *R. catesbiana,* the foreign species not only failed to inhibit, but in most cases caused the tadpoles to grow more rapidly. Curves comparing growth rates of tadpoles with and without *Physa* (Figure 2) and with and without *Necturus* (Figure 3), are presented.

It should be noted that the weights in the experiment with *Physa* are total weights. Although 4 tadpoles weigh more than 2 at any one time, the average weight for one tadpole in a group of 4 is always less than the average weight of one growing in a group of 2. In both cases the tadpoles grew better when the foreign animals were added. Reason for believing that this is not a direct stimulation by the *Physa* and *Necturus,* but rather a removal of tadpole inhibition by them will be detailed elsewhere. The basis of the belief is that *Necturus* and *Physa* further tadpole growth only when they are in the same container with the tadpoles. Water from *Necturus* or from *Physa* is ineffective. It appears likely that the

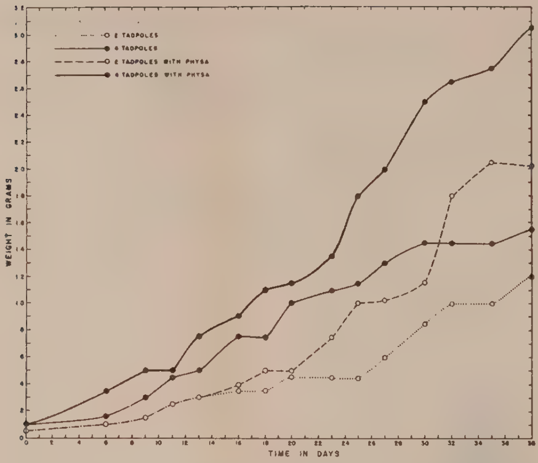

FIG. 2. Growth curves of 2 tadpoles and 4 tadpoles growing with and without 6 *Physa* in one liter of water which was changed daily. Weights are total weights of tadpoles.

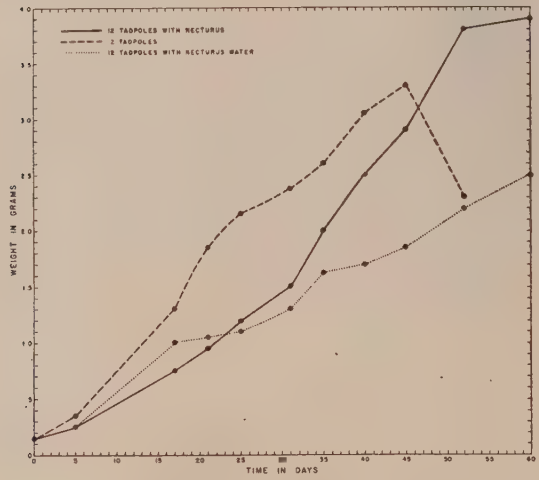

FIG. 3. A plot of average weights of tadpoles in a group of 2, in a group of 12, and in a group of 12 living with *Necturus*. The drop in the curve for 2 came at metamorphosis.

foreign organisms can metabolize away the growth retarding feedback products of the test tadpoles.

DISCUSSION

It is clear from the data presented by Richards (1958), and the experiments described in this article, that large rather specifically inhibitory particles appear in the culture water of growing tadpoles. The "Lebensraum" or crowding effect can now be wholly explained as a consequence of the production of these particles.

Before growth inhibiting products had been demonstrated, mutual agitation had been invoked to explain decreased growth under crowded conditions. It seemed the only possible explanation of certain experimental results. Rugh (1934) and Lynn and Edelman (1936) had studied the growth of tadpoles in aquaria divided into compartments by wire screens. Different numbers of tadpoles in the compartments grew at different rates. Average weight decreased with crowding within the compartment. This seemed to eliminate as agents of growth control any water borne substances. The tacit assumption was made that any water borne substance would become equal in all compartments. This is not true of continuously produced substances in the absence of instantaneous mixing of the waters of the compartments. So long as there were different amounts being produced in the different compartments, concentrations would differ and growth rates might differ. However slight the concentration differences may have been, if they were sufficient to affect growth rate at all, a great difference in growth would finally become apparent. Superimposed on the original growth differences would be the differences arising from the fact that larger inhibit smaller much more than smaller inhibit larger. Once differences arise the larger tend to pull farther and farther ahead.

The compartment experiments showed that there were appreciable differences in growth rate in the partially isolated compartments, but they did not demonstrate a lack of influence of animals in one compartment on those in another. Adequate controls, the same numbers in the same volumes but not receiving any water from tadpoles in other compartments, were not used.

Although an agitation factor or a psychological factor was suspected for many years, it was never demonstrated. It was a suggestion which arose because no other explanation seemed possible. Adolph (1931) learned that tadpoles kept in motion in cloth bags did not grow. The treatment, however, was so drastic that skin was rubbed off. The conclusion that agitation of the type and amount caused by tadpole collisions might decrease growth does not follow from such an experiment nor has it ever been demonstrated. Furthermore, a social factor would not account for the fact that single tadpoles grow at a rate which is proportional to the size of their container. Growth products would reach inhibitory concentrations sooner in small containers. A feedback system seems sufficient to account for all the known facts.

Hodler (1958) writing just before the work of Richards appeared has again suggested some non-chemical social factor. He transferred culture water in which tadpoles had been growing to assay tadpoles and found no effect, but the water was filtered before it was assayed. Simple filtration through paper removes all inhibitory material (West, to be published).

The specific inhibition hypothesis apparently originated as an explanation of crop failures of the kind which can be prevented by rotation of crops. By 1832 enough practical agricultural knowledge had been amassed so that de Candolle could distinguish the effects of over-cropping which led to depletion of soil nutrients and a rather specific effect when the same species was planted a second year in the same soil. After general depletion no crops did well, whatever the species. After the more specific effect only members of the same family grew poorly. Members of other families grew well.

De Candolle explained the specific effect as specific inhibition. The plants were thought to excrete to the soil substances which interfered with their own growth and that of their close relatives without affecting the growth of more distantly related plants. Already in 1832 there was the beginning of an experimental basis for this belief. De Candolle cites the experiment of a M. Macaire who had learned that kidney beans do not develop in water which had previously bathed the roots of kidney bean plants, but that wheat grows very well in the same water.

During much of the 19th century and during the first half of the 20th another explanation of the beneficial effects of crop rotation became dominant (cf. Klaus 1939). A particular crop was thought to remove trace elements, nutrients and unknown growth factors. These could be replenished during the growth of another crop that did not have the same requirements. It is true that certain plants do require more of certain trace elements than others, and that some plants, for example legumes with their nitrogen fixing bacteria, can replace nutrients which others have removed.

In spite of the truth of the above statements, the specific depletion hypothesis has become unacceptable. The first reason is that there are more plant species which change the soil specifically than there are elements and growth factors which the plants cannot themselves produce or which are not supplied in adequate amounts in fertilizers. Yet fertilizers do not remove the specific effect.

There is another reason why any depletion theory is unacceptable. All of the substances necessary for excellent plant growth are contained in a mixture of virgin soil and fertilizers. After a plant has grown in it the mixture is no longer good for the same plant, but remains good for other kinds. If just allowed to stand the soil becomes good again for the original kind of plant. This cannot be explained as a depletion unless it is a depletion which can be rectified by something from the air. Quantitative difficulties arise again. There are not enough gases in the air to make up for the many different specific effects. Instead, the evidence suggests the addition of specific toxic agents that decay in time.

It is only in recent times that such agents have been demonstrated satisfactorily by good, direct experiments. It is seldom that trees can be replaced by the same kinds of trees and do well. For example, young peach trees do not grow well in cut over peach orchards. Peaches may be used to replace apples and other kinds of trees, but young peaches fail where older peaches have been. Other kinds of trees replace peaches satisfactorily (Proebsting 1950, Koch 1955). Virgin soil that supports good growth of peaches no longer does so when small amounts of peach root are added (Proebsting and Gilmore 1940). Patrick (1955) has demonstrated that amygdalin from peach roots yields HCN and benzaldehyde, but it is doubtful that any such general inhibitors could account for the very specific peach effect. Regardless of the specificity of these particular substances, peach specific growth inhibitors produced by peach trees have been demonstrated.

The guayule plant manufactures cinnamic acid which acts as a guayule inhibitor, but it is not known how specific this is or whether it is effective under field conditions (Bonner 1950).

Excellent evidence that cereals inhibit cereals under field conditions has been presented by Schönbeck (1956). Cereals produce substances which are more inhibitory to cereals than to other plants. These can be extracted from soils where cereals had grown. Concentrations of extracts which inhibit the germination and development of cereals actually stimulate the germination of some other kinds of plants. Specifically inhibitory substances reach peak concentrations in fields of stubble during December and January. Microorganimisms decompose the inhibitors, but a high enough concentration remains to be partially effective at the time of spring planting.

It is quite clear now that plants and tadpoles are rather specifically inhibitory, but in addition there is much scattered information indicating the universality of the phenomenon.

Pasteur was probably the first to recognize that bacteria stopped their own growth before nutrients were exhausted by adding something to their medium (Dubos 1950). Braun (1952, 1958) was able to demonstrate that bacteria producing a particular amino acid stop growing when that acid reaches a certain concentration. By adding the amino acid in that concentration, growth can be stopped at any point on the growth curve. Other workers now find that not only amino acids, but also purines and pyrimidines act in a negative feedback fashion to limit specific enzymes involved in their production (cf. Magasanik 1957).

Not as much is known about substances involved in growth limitation in other kinds of organisms, but it is certain that rather specific inhibitory products are involved.

Diatoms release products of metabolism which build up to growth inhibitory levels. If nutrients are added, products removed and the numbers of the diatom *Nitzschia* kept at a certain high level, maximum production can be maintained for long periods. Without removal of excess organisms and products growth always stops (Ketchum and Redfield 1938).

It is quite generally known that Protozoa are self-limiting (cf. Allee *et al.* 1949). Woodruff (1913) explained succession of species as due primarily to the accumulation of a succession of species-specific inhibitory products. Separation of inhibitory and stimulating substances from the culture medium of *Tetrahymena* has been demonstrated (Kidder 1941).

Other animals known to limit growth and/or reproduction of members of their own species when living in the same water are *Hydra* (Loomis and Lenhoff 1956), *Planaria* (Goetsch 1924), snails (Hogg 1854, Colton 1908, Crabb 1929), *Daphnia* (Warren 1900, Langhans 1909), echinoderm larvae (Vernon 1899), and mosquito larvae (Roubaud 1923).

Both for echinoderm larvae (Vernon 1899) and *Daphnia* (Langhans 1909) it has been shown that the products are relatively specific. In both groups of animals the water from one species is most inhibitory to members of the same species, less so to members of closely related species, and serves as an excellent culture medium for members of more distantly related species in other families.

Sang (1950) reviewed evidence indicating that animals in general and *Drosophila* in particular are self-limiting. One of the consequences of an increase in population density is a decrease in fecundity. It is apparent that this is one of the general phenomena associated with life. Different explanations have been offered for different cases. These are really untested hypotheses. Such a general phenomenon may be the result of a general mechanism. There is some indication that at least for aquatic organisms rather specific products may control fecundity. Langhans (1909) learned that the number of hatched *Daphnia* which could survive depended on a water-borne product and that since fecundity varied in the same way as survival it was presumably controlled by the same factor. Experiments with the guppy, *Lebistes reticulatus,* also indicate that the number of young produced and the number which survive is controlled by a water-borne product (Rose 1959).

Another question requiring further study is why fish in ponds and lakes are stunted when the density of fish is high. The assumption was made many years ago that control was exercised by the amount of food available. That this cannot be the only factor is apparent from the fact that the rate of growth of ciscoes in lakes where much food is present varies but is independent of the abundance of food (Hile 1936). Similarly Johnson and Hasler (1954) learned that in a series of lakes the trout grew least in that one where they were most dense in spite of the fact that food organisms were as numerous or more numerous than in the other lakes. In laboratory and hatchery experiments where food has apparently been eliminated as a factor (Church 1927, Willer and Schnigenberg 1927, Shaw 1929, Yoshihara 1952) growth is in some way controlled by a density factor.

The same effect of large on small as demonstrated for tadpoles was also observed in growing trout (Brown 1946). Trout fry were kept in 2 aquaria with a continuous flow of water. In both aquaria individuals grew at different rates and marked differences in size resulted. As with tadpoles the smallest individuals died. After a few months the larger trout from both aquaria were regrouped in one aquarium and the smaller ones were placed together in another aquarium. The smaller in the new group of larger fish then grew more slowly. The largest in the new group of small fish grew very rapidly and after a few months were almost as large as the largest in the group of larger fish.

Apparently food was not the limiting factor. An excess of food was present most of the time. The larger trout did not appear to inhibit feeding by smaller ones in any overt way. Margaret Brown concluded, "The lower growth rates of smaller fry can be attributed to some 'social organization' within the group, those which began to feed earlier attaining a higher position in the hierarchy than the others and therefore continuing to grow at higher specific rates." At the time, 1946, it had not yet been demonstrated that chemical feedbacks involving very low concentrations of products are effective in bacteria. Novick and Szilard working with a bacterium that excretes an amino acid as an end product found in the Chemostat where the medium is constantly replaced that the amino acid controlled its production at concentrations of the order of one microgram per liter (Novick 1955). Recent studies (Rose 1959 a and b) indicate that fish growth and reproduction may be controlled in feedback fashion by water-borne products.

In most of the cases noted above growth decreases as the organisms add something to their culture medium. The feedback mechanism is relatively specific in those few cases where the specificity is known.

In tadpoles a long lasting particle, possibly a cell, is involved in growth control (Richards 1958). This is not universally true. Small molecules may be the agents of control in bacteria (Braun 1952, Cohn, Cohen and Monod 1953, Davis 1954, Novick 1955, Magasanik 1957). Neither is it universally true that a long lived product is involved. Even though large snails of the genus *Ampullaria* inhibit small ones in the same culture dish with much food, culture water from that dish does not inhibit the growth of small snails in another dish (Rose, in progress). If an inhibitory product is involved it is short lived and its effect is not noted when culture water is added only once a day.

There are 3 suggestions concerning the mechanism of specific inhibition. The first is that products, anti-templates, may neutralize the templates producing them (Weiss 1947, 1955, Weiss and Kavanau 1957). James D. Watson in a lecture in 1958 at the University of Illinois suggested along this line that proteins might collect on their nucleic acid templates and prevent further production at the occupied sites.

The second suggestion is that, as in ordinary chemical reactions, products if not removed may act in the mass action relationship to limit their further production (Rose 1952, 1957).

The third suggestion is that products as they accumulate act in a feedback system to limit the formation of an enzyme necessary for their production. This has been demonstrated for bacteria as noted above.

With our biochemical knowledge still quite fragmentary concerning self-limiting processes, it is still too early to eliminate any of the three suggestions. Certainly the enzyme limitation method has been demonstrated, but it may be effected through the mass action relationship and template clogging.

The fact that a species may be less self-limiting when another species is present in the same water indicates that one may remove the inhibitory products of another. The beneficial effect is over and above what is known as conditioning of the medium. A conditioning species adds something to the culture medium. It is not necessary for the conditioners to be in the same container with the recipients. For the effect as reported here the second species must be present in the same container. Water from the second species does not relieve the self-inhibition of the first. Mutual benefits derived from relief of inhibition may account in part for the survival value of communities of very different kinds of organisms.

The fact of self-inhibition may also account for the common observation that growth is better if water has been conditioned by a foreign species. Goldfish can condition the water for others of their own species, but the conditioning period is short (Allee *et al.* 1934). Supposedly if organisms are a long time in water, not only have they added valuable materials to the water, but they have also added products which will inhibit members of their own species.

Conditioning organisms may also serve to remove generally toxic materials such as lead ion (Allee *et al.* 1949). Bilski (1921) studying the growth of tadpoles did not observe that changing water enhanced growth. From our vantage point now we suspect that his water contained toxic material which overcame the beneficial effect of removal of products.

The fact that slowly growing members of tadpole and fish populations fail to survive even in the presence of much food suggests that this type of control might lead to rather rapid evolutionary change (Rose 1959). A genome resulting in rapid growth in a particular environment might quickly become the wild type there since its bearers would be suppressing their more slowly growing relatives. Here again more work is needed, especially in the field.

SUMMARY

Growth rates and size at metamorphosis of *Rana pipiens* tadpoles fed maximally increase with container size over the range studied.

When different numbers of tadpoles all from the same egg mass are cultured in containers of the same size, the average growth rate is inversely proportional to the number of individuals. However, those which get ahead in all containers of the same size grow equally well regardless of the number of smaller individuals in the same container. The average growth rate decreases with

increase in number of individuals not because all individuals are stunted but because more are.

When small and large individuals are cultured together under conditions allowing excellent growth of either alone the small fail to grow. Stunted individuals removed from their larger partners grow well; if not removed they die.

The growth retarding effect passes from one individual to another through the water. Culture water taken from larger tadpoles and used for smaller ones inhibits the smaller. The agent of inhibition is long lasting at room temperature, but disappears rapidly at temperatures above 60°C.

Inhibition is rather specific. *R. catesbiana,* a member of the same genus inhibits *R. pipiens,* but the salamanders, *Notophthalmus* and *Necturus* do not, nor do several fish and snails. These foreign organisms typically reduce the effect of *R. pipiens* on *R. pipiens.*

Evidence indicating that rather specific growth inhibition is general among aquatic animals and terrestrial plants is reviewed. Both growth rate and population size seem to be regulated in a limited aqueous environment in negative feedback fashion.

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REFLECTIVITY OF THE INTEGUMENTS OF SOME LIZARDS FROM DIFFERENT HABITATS

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Introduction

The role played by the integument of lizards in thermoregulation has received considerable attention, especially in recent years. Parker (1934) speculated on the function of melanism in lizards and attempted to correlate it with climatic conditions. Atsatt (1939) studied the effects of temperature and light on the color changes of 16 species of desert lizards from southern California. Klauber (1939) discussed the part played by coloration of reptiles in the southwestern United States in climatic and concealing adaptations. The toleration of desert reptiles to solar radiation was examined by Mosauer and Lazier (1933) and Mosauer (1936). An experimental method for studying the effects of radiant energy on lizards was described by Cole (1943). He determined the lethal temperatures of 10 species and demonstrated that dark colored animals were more easily overheated than light colored animals. Cowles and Bogert (1944) examined the thermal requirements of 19 species of reptiles from the southwestern United States and discussed the functions of behavioral and physiological mechanisms, and coloration in the thermoregulation of reptiles. Bodenheimer, Halperin, and Swirski (1953) measured the transmission of light through the skin of the eyed skink, *Chalcides ocellatus.* The only published measurement of reflectivity of lizard integuments known to us is that of Norris (1958). He measured the albedo through the visible range of the spectrum from the dorsal skin of the lizard genus *Uma* and found that the reflectivity curves matched those of the dune sand on which the animals lived.

As pointed out by Cole (1943), the publication in 1939 of Cott's book, "Adaptive Coloration in Animals," resulted in widespread interest in the concealing coloration of animals. This interest in visual benefits of coloration may have been overemphasized, with the physiological benefits either being denied or neglected.

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Renewed interest since the early forties has served to stimulate much thought and work on these 2 aspects of coloration, especially its role in thermoregulation. Opinion is still divided as to whether or not Gloger's rule (1833), that animals show a gradient in melanic pigmentation from light to dark between areas of low humidity and temperature to those areas of high humidity and temperature, is an expression of concealing adaptation of color or of a physiological adaptation for thermoregulation (Cowles 1958). At the present time few definitive answers have been found with respect to this problem of coloration in lizards. Undoubtedly both aspects are involved, but much work remains to be done.

This paper is an attempt to compare the reflectivity of the integuments of lizards from different habitats and to discuss the results in terms of environmental adaptations.

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Materials and Methods

Twenty-six individuals of 16 different species of lizards were used in determinations of skin reflectivity. These animals were collected by the authors, purchased from animal dealers, or supplied by other collectors. The animals were kept in the laboratory at 21°-23°C and were used as soon after receipt as possible. Skin from the mid-dorsal and mid-ventral portions of the body was removed, cleaned of underlying fascia and muscle, and placed on small squares of damp brown paper toweling. Some contraction of the skin occurred after removal but the skin was restretched to approximately the same degree as that remaining on the animal. For 3 of the smaller species (*Anolis, Lygosoma,* and *Hemidactylus*) a mosaic of 2 or 3 pieces of skin was constructed. This procedure was necessary because a minimum circular surface of approximately 18 mm diameter was required in measurement. Reflection from the integument was measured by use of a Beckman Model DU quartz spectrophotometer equipped with a reflectance attachment. Monochromatic reflectance was obtained at a 90° angle to the skin surface, using a magnesium carbonate block as a standard. A magnesium carbonate block has a reflectivity of 97% or more over the wave lengths used in these determinations. Correction curves for magnesium carbonate can be obtained from Benford, Lloyd, and Scharz (1948).

Readings were taken at not more than 20 mμ intervals over a spectral range from the far ultraviolet (320 mμ) to the near infrared (1100 mμ). Reflectivity values were obtained at intervals of 10 mμ when the curves increased or decreased rapidly and at comparatively sharp peaks. The entire curve for one run usually required 30 minutes for completion. After the initial determinations a few points along the curve were checked for possible changes of the skin during the run which could effect changes in the albedo. In no case did these changes amount to more than 5%, and in most cases the changes were appreciably less, averaging about 1.5%. Attempts to define the colors of experimental animals before and after experimental runs, by using a color dictionary (Maerz and Paul 1930), were generally unsuccessful. Color dictionaries "are not useful for the definition of dorsal coloration . . . , because the color results from the summation of a series of color patterns superimposed one upon another. The component colors are of minor importance compared to the resultant blended color" (Norris 1958). This statement was applied to lizards of the genus *Uma,* but it is also true of any animal with superimposed color patterns such as those found in most lizards.

Averages of the reflectance readings were used for the mean values since they were found to be almost identical to those determined by planimeter integrations of the entire reflectivity curves.

Geographic ranges of the North American lizards may be found in Schmidt (1953) and Stebbins (1954). The animals studied are listed below by habitat.

Results

Description of Habitat and Reflectivity Curves

Callisaurus draconoides gabbi—The Colorado Desert gridiron-tailed lizard occurs in the Lower Sonoran Life-zone on desert flats which usually contain small rocks, or, sometimes, on rather rocky areas, but favoring sandy areas of dune margins and desert washes (Stebbins 1954). Usually they are active in the early morning until approximately 10:00 A.M. and again in late afternoon, thus avoiding the hottest part of day. These periods of activity are modified on cool days and at cool localities, the lizards emerging later and retiring earlier in the day. A body tempera-

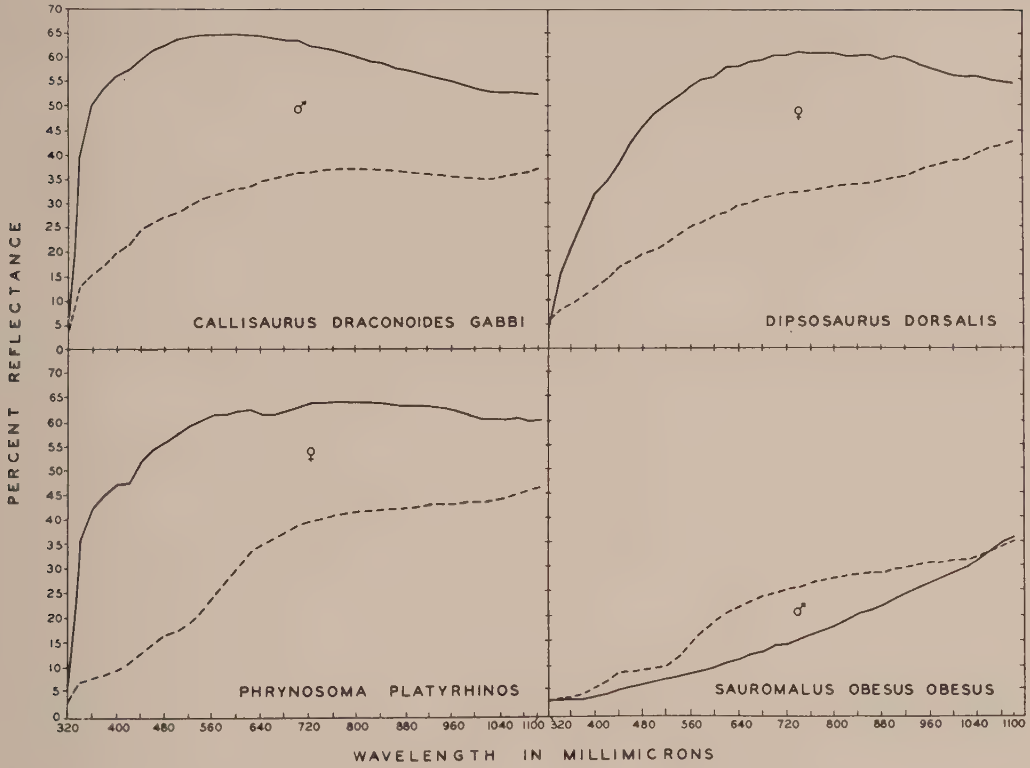

FIG. 1. Reflectivity of 4 desert species. Solid lines, ventral integument; broken lines, dorsal integument.

ture of approximately 47° C is lethal (Smith 1946). This species is generally light gray in dorsal coloration, but is darker at temperatures below 40° C. This color change is apparently not influenced by the color of the substratum (Atsatt 1939). The average reflectivity of the ventral skin of a single adult male from Edwards, California, over a spectral range from 320 mμ to 1100 mμ was 56.1%, and of the dorsal skin, 31.4%. The peak reflectivity of the ventral skin occurred in the middle of the visible range, while the dorsal integument showed a gradual increase with a maximum in the near infrared (Figure 1).

Dipsosaurus dorsalis—The northern crested lizard occurs in the Lower Sonoran Life-zone on flat areas of the Colorado and Mojave Deserts. There are a few nocturnal records for this lizard, but it is most often diurnal in habit, being active later in the day than many other desert lizards. This habit of late emergence may be due to its larger size, requiring a longer time for the heat gain to produce an optimal temperature and also, possibly, to the habit of plugging its burrow at night, thus slowing heat penetration to the animal (Stebbins 1954).

The normal activity range extends from 34° to 41° C, with a critical maximum of 47°-47.5° C (Cowles and Bogert 1944). The general dorsal color is a grayish brown. The animal is darker at temperatures below 24° C and light does not effect the coloration at the lower temperatures (Atsatt 1939). Reflectivity of the dorsal skin of an adult female, locality unknown, averaged 28.4%, with a gradual increase to 42.0% at 1100 mμ. The ventral skin had a mean reflectance of 51.1%, with a maximum reflectance in the upper visible and near infrared regions (Fig. 1).

Phrynosoma platyrhinos calidiarum—The desert horned lizard is found in the Lower and Upper Sonoran Life-zones of the Colorado and Mojave Deserts and the Great Basin. They are active through most of the day, although in areas which become too hot, the lizards submerge into the sand. Cowles and Bogert (1944) report an activity temperature of about 36.8° C, a maximum voluntary tolerance of 39° C, and a retreat from cold at 29° C. The dorsal ground color of the animal used was grayish brown and the ventral color, cream. Atsatt (1939) found that the color of species of this genus is dependent upon temperature, primarily, and upon illumination, secondarily. At the higher temperatures the animals are always

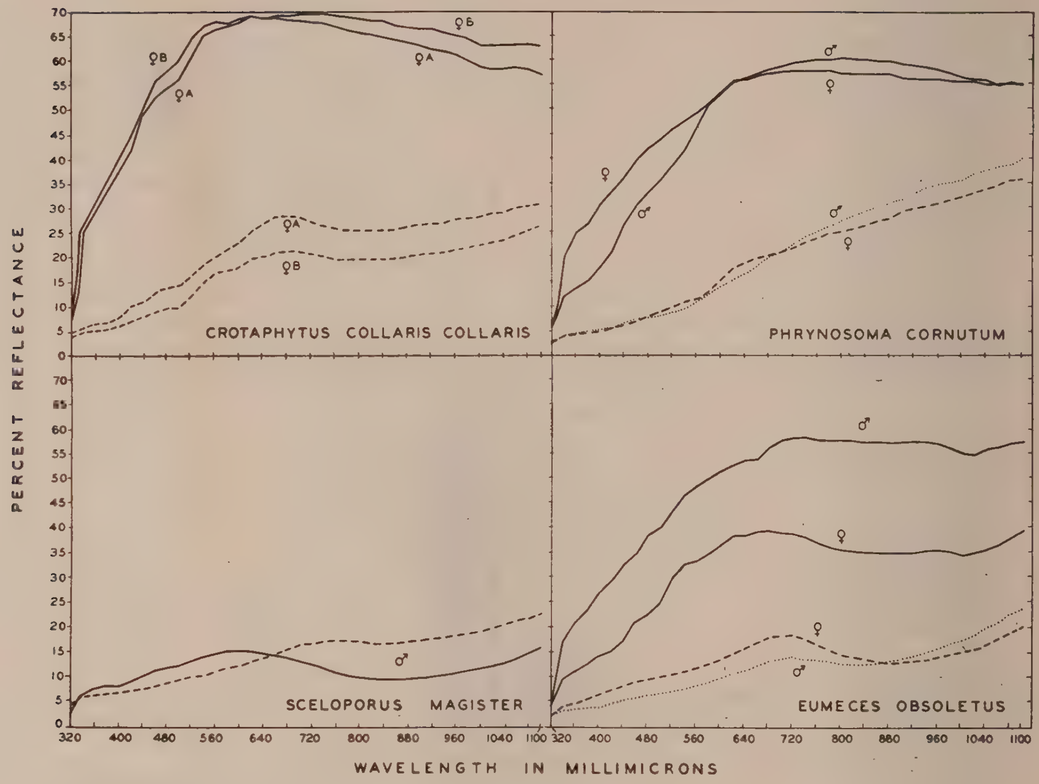

Fig. 2. Reflectivity of 2 desert, one semi-desert and one plains species. Solid lines, ventral integument; broken lines, dorsal integument.

light in color and at lower temperatures, dark in color. At intermediate temperatures (27° C), however, the animals become dark under illumination and light under conditions of darkness. This appears to be true of many iguanids. An adult female from Edwards, California, had an average reflectivity of 32.3% for the dorsal skin and, 57.2% for the ventral skin (Fig. 1).

Sauromalus obesus obesus—The chuckwalla is an inhabitant of the Lower Sonoran Life-zone with a range and habitat very similar to that of *Phrynosoma platyrhinos*. During the day they bask on rocks or boulders and seek refuge in the cracks and crevices at night, or when disturbed. Cowles and Bogert (1944) found an average activity temperature of 37.7° C, with a maximum voluntary temperature of 42° C, and a critical maximum of 43.3-49° C. The color changes with temperature and illumination are similar to those of *Phrynosoma* (Atsatt 1939). The adult female used in this experiment was collected at Panarama City, California. The brownish gray dorsum with traces of juvenile crossbands, had a mean reflectivity of 21.6% with a gradual increase through the measured range. The dull red ventral surface had an average reflectivity of only 16.3%. This was the only case among the lizards studied, with the exception of male *Sceloporus*, where the reflection from the ventral surface was less than that from the dorsal surface.

Crotaphytus collaris collaris—The collared lizard resides in the rocky mountainous or hilly areas of the arid or semiarid region in the Upper Sonoran and Transition life-zones. It appears to prefer rocky areas and is found in the plains only where canyons, gullies, or rock piles provide suitable habitat. Fitch (1956) found collared lizards active within a range of 13.5°-36° C air temperature, with more than half occurring within a range of 28-33° C. A temperature of 45° C was not lethal. Atsatt (1939) found that *Crotaphytus collaris baileyi* was dark at low temperatures, light at high temperatures and light or dark, depending upon illumination, at intermediate temperatures. Two adult females from Harper, Kansas, had average reflectances of 17.0% and 21.5% for the dorsal surfaces and 58.2% and 56.4% for the ventral surfaces. Both animals were light yellowish green in dorsal coloration and cream in ventral coloration. The curves for both individuals show a slight peak at 640-720 mμ (orange-red), although these colors were not evident in the overall coloration of the live animals (Figure 2).

Phrynosoma cornutum—The Texas horned lizard is found on open flat terrain in sandy or rocky areas in the Lower and Upper Sonoran life-zones. Although many aspects of the biology of this species have been studied extensively, little has been reported on temperature relations. Both animals examined were brownish red in dorsal ground color and cream to white in ventral color. An adult male from Abilene, Texas, had a mean reflectivity of 20.2% for the dorsal surface and 48.3% for the ventral surface. There is no great difference between the curves of the male and female (Fig. 2).

Sceloporus magister magister—The desert spiny lizard occurs principally in the Lower and Upper Sonoran life-zones. This species is usually absent from open desert or plains, preferring rocky areas with vegetation which provides suitable cover, for example, cottonwood, willow, yucca, cacti, and creosote bush. It is semi-arboreal in habit. Cowles and Bogert (1944) found that individuals of this species preferred air temperatures of 30°-33° C, with a body temperature approximately 4 degrees higher. Atsatt (1939) has shown that color change is directly correlated with temperature at the extremes, but at intermediate temperatures the color is dependent on illumination and psychological factors. An adult male from Panarama City, California, had an average reflectivity of 14.5% for the dorsal integument and 11.6% for the ventral skin (Fig. 2). The comparatively low value obtained for the ventral surface was mainly due to the blue lateral abdominal patches characteristic of males in this genus.

Eumeces obsoletus—The Great Plains skink is most often found under rock slabs or in rock crevices in both wooded and grassland plains of the Upper Sonoran and Lower Transition life-zones. This is a secretive diurnal species. Fitch (1955) concluded that the optimum temperature range for this speices was between 31° and 34° C. He also reported some activity of this lizard at temperatures of only 7° C in the laboratory, and one individual was seen basking under natural conditions at an air temperature of only 12° C, far below the reported activity ranges of desert species. An adult male from Chanute, Kansas, had a mean reflectivity of 13.0% for the dorsal surface and 48.2%, for the ventral skin. An adult female from the same locality had values of 11.4% for the dorsal skin and 30.9% for the ventral surface. The female was unusual in being dark gray in ventral coloration, resulting in a rather low reflectivity curve in comparison with the male (Fig. 2).

Anolis carolinensis carolinensis—The green anole is largely arboreal and diurnal, being most active in the early morning hours. This lizard occurs in the Lower Austral and Tropical life-zones. The metachrosis of this species has been studied extensively (Kleinholtz 1938, Parker 1943, Walls 1952). At low temperatures the animals are usually dark and the color is not influenced by light. At high temperatures several factors may produce color changes. Lack of illumination results in a green color, as do factors of psychological stress, such as fighting. Illumination of the skin at high temperatures results in a dark chestnut color due to the expansion of the choromatophores. This expansion is increasingly inhibited by the amounts of green light entering the eyes. In pure green light, the animals are green in color. They usually also turn green at death. The individuals used in this experiment, however, were a light brown at death, with a scattering of very light green patches on the dorsal skin, a condition often seen in live animals as they change from a brown to a green color at times of excitement. A mosaic of 3 dorsal skin pieces of adult males and females from Wauban, Louisiana, averaged 10.0% and 10.7%, respectively, with a peak in the yellow-green portion of the spectrum. The ventral skin mosaic of the females averaged 26.0% in reflectivity, while that of the males was 33.2% (Figure 3). This difference between the sexes is probably largely due to metachrosis rather than to sexual dimorphism.

Lygosoma laterale—The small, slender ground skink is an inhabitant of wooded areas where it may be found on the forest floor. They occur in the Upper and Lower Austral life-zones, reaching into the Tropical Life Zone in southern Florida. This is apparently a diurnal species, although unconfirmed reports suggest they may also be nocturnal to some degree (Smith 1946). A skin mosaic of two pieces from two different adults was required for a measurement of reflectance. Care was taken to match the dorsal brown areas and lateral stripes on the dorsal skin mosaics. The dorsal surfaces had an average albedo of 10.7% for the males and 8.6% for the females. The ventral skin mosaic averaged 28.6% for the males and 22.8% for the females (Fig. 3). All of the specimens used were collected near Wauban, Louisiana.

Ophisaurus ventralis—The eastern glass lizard occurs in the Upper and Lower Austral life-zones, though most of its range is within the latter life-zone. It is usually an inhabitant of moist

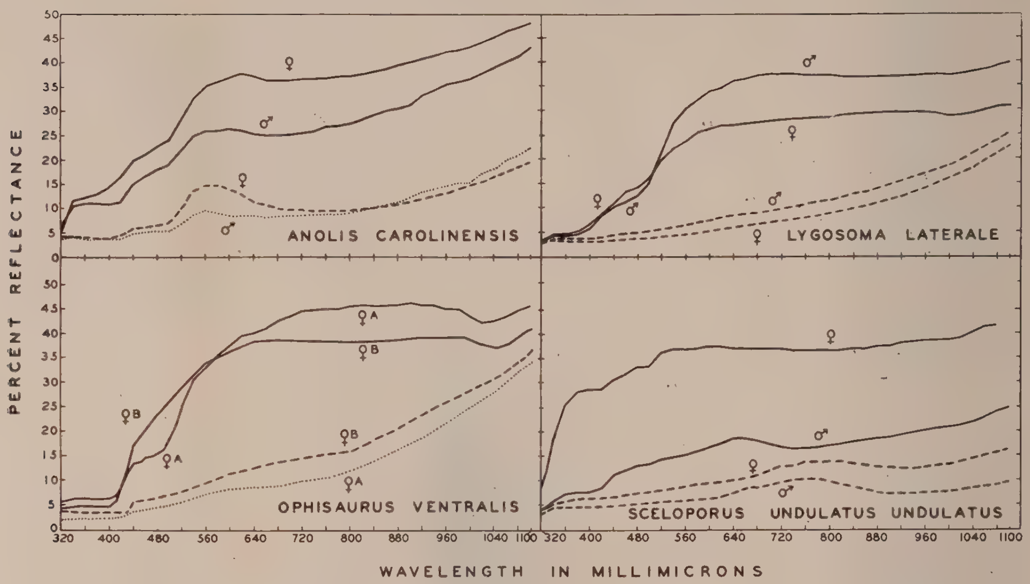

FIG. 3. Reflectivity of 4 species from eastern and southeastern forests of the U. S. Solid lines, ventral integument; broken lines, dorsal integument.

meadows, grasslands, or pine flatwoods. These lizards have been observed abroad at night as well as during the day. Two adult females from Beaufort, North Carolina, had average reflectance values of 14.7% and 12.1% for the dorsal skin and 28.0% and 32.1% for the ventral skin. In both females a slight "dip" occurred in the curve of the ventral skin at approximately 1060 mμ (Fig. 3).

Sceloporus undulatus undulatus—The southern fence lizard is common in the Lower Austral Life-zone where it is frequently seen on sandy pine lands, especially on fallen timber, stumps, fences, and piles of wood. This is partly an arboreal and strictly a diurnal species. The average albedo of the dorsal skin of an adult male was 7.2% and of the ventral skin, 16.1%. An adult female averaged 10.8% and 34.3%, respectively (Fig. 3). Both animals were collected at Ocala, Florida.

Sceloporus undulatus hyacinthinus—The northern fence lizard occurs primarily in the Upper Austral Life-zone. They are similar in habit and habitat to the southern race. Reflectivity measurements of *hyacinthinus* were very close to those of *undulatus*. An adult male from Durham, North Carolina, averaged 11.4% for the dorsal skin and 15.7% for the ventral skin. An adult female from the same locality averaged 10.8% for the dorsal integument and 34.3% for the ventral skin (Figure 4). As in the other *Sceloporus* the sexual dimorphism in ventral coloration resulted in low reflectivity in the males.

Sceloporus woodi—The Florida scrub lizard occurs in the Lower Austral Life Zone of the central part of the Florida peninsula. It is a characteristic inhabitant of the "rosemary scrub in the more open 'strands'" (Carr 1940). This is a cursorial species, but it is also a rather good climber, ascending trees to a height of 20 or more feet. An adult male from the vicinity of Ocala, Florida, had mean reflectance values of 10.0% for the dorsal skin and 14.9% for the ventral skin (Fig. 4). These values are very similar to those of both races of *S. undulatus*.

Lacerta muralis—The European wall lizard is an inhabitant of western Europe where it is a common element of the fauna. It often frequents human habitations and fences. Two adults from Chemnitz, Germany, were used in this experiment. The male averaged 7.4% in the albedo of the dorsal skin and 29.6% in the ventral integument. The female had values of 7.2% and 13.8% for the dorsal and ventral skins, respectively.

Hemidactylus brookii haitianus—The western house gecko is pantropical in distribution, with four geographic races being recognized (Loveridge 1947). It is strictly a nocturnal species, with vertical pupils and a translucent skin. In areas of the West Indies where it occurs, it is most often found about dwellings and other buildings. The animals used for reflectivity measurements were a light tan in ground color. A dorsal skin mosaic of 2 pieces of adult males from Rio Piedras, Puerto Rico, had an average reflectivity

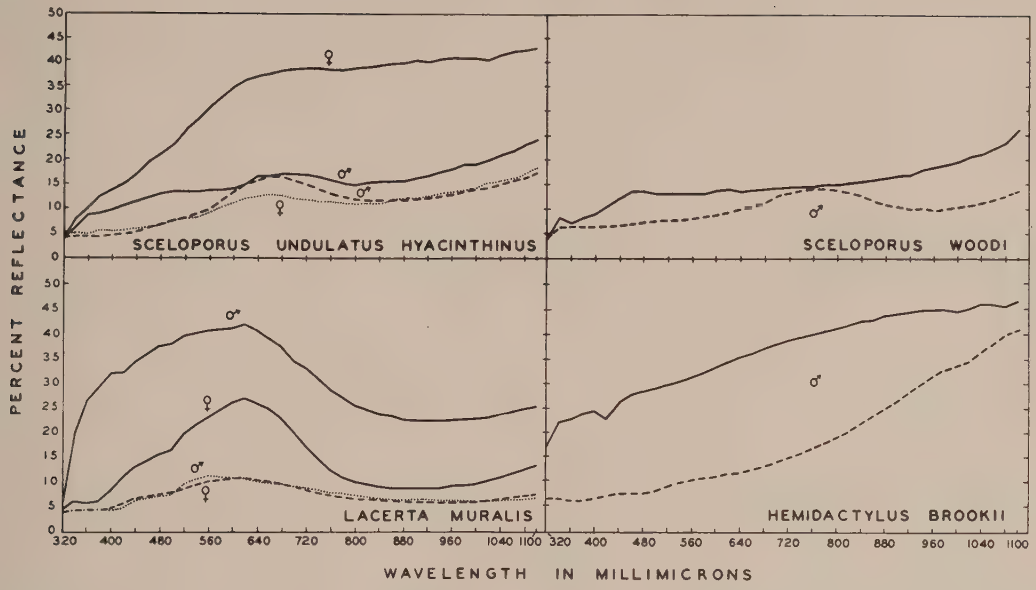

FIG. 4. Reflectivity of 2 species from eastern and southeastern forests of the U. S., one species from European temperate forests, and one species of a tropical gecko. Solid lines, ventral integument; broken lines, dorsal integument.

of 18.4% for the dorsal skin and a value of 86.3% for the much lighter colored ventral integument (Fig. 4).

Iguana iguana—The large common iguana of tropical America (from southern Mexico through tropical South America and the West Indies) prefers a habitat in the gallery forests along streams. This is an arboreal species, climbing high trees from which they may plunge when disturbed, into a nearby stream. A juvenile female of unknown locality was dark greenish-brown in dorsal color, giving an average reflectance of only 6.2%. The ventral surface was bright yellowish-green in color, with the greatest reflectivity in the green region of the spectrum, producing a high peak of 560 mμ. The average albedo of the ventral surface was 21.7% (Figure 5).

CALCULATED HEAT GAINS OF DORSAL SKINS

A direct comparison of the mean reflectances of the species studied may be misleading. The energy content of radiation in the solar spectrum is unevenly distributed. This distribution at sea level is given in Table I for optical air masses[3] 1 (high transmission) and 5 (lower transmission) in cal/cm^2 min. The values in Table I were taken from the Smithsonian Meteorological Tables, Sixth Edition (List 1951).

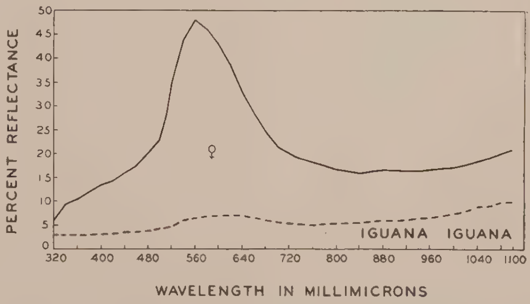

FIG. 5. Reflectivity of the skin of the common iguana from gallery forests of the tropics. Solid line, ventral integument; broken line, dorsal integument.

TABLE I. Energy content of solar radiation at sea level. Values in cal/cm^2 min; percentages of the energy content of each band of the spectrum are given in parentheses

Wavelength mμ	Air Mass 1	Air Mass 5
290-400	0.059 (4.3%)	0.004 (0.6%)
400-700	0.616 (45.2%)	0.240 (38%)
700-1100	0.454 (33.3%)	0.266 (42.2%)
1100-1500	0.140 (10.3%)	0.060 (9.5%)
1500-1900	0.075 (5.5%)	0.052 (8.2%)
1900-∞	0.019 (1.4%)	0.009 (1.4%)
Total	1.363	0.631

The energy content of solar radiation below 290 mμ is extremely small. The visible range (400-700 mμ) contains 45.2% of the heat energy with

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[3] An optical air mass is defined as the length of an atmospheric path traversed by the sun's rays in reaching the earth, measured in terms of the length of this path when the sun is in the zenith.

an air mass of 1 and 38% with an air mass of 5. The near infrared (700-1100 mμ) also contains a rather high percentage of the energy, 33.3% and 42.2% for air masses of 1 and 5, respectively. These 2 segments of the spectrum account for 79 to 80% of the total energy.

This information on the energy content of various segments of the solar spectrum at sea level offers a convenient method for comparison of our data on dorsal skin reflectances. The product of the average % absorption from 400 to 1000 mμ and the energy content of the same spectral range (from Table I) gives an average heat gain from solar radiation in cal/cm² min.

Table II gives the calculated average heat gain of the dorsal integuments of the lizards studied. A correlation of heat gain and habitat is clearly evident, the desert species having the lowest and the tropical iguana, the highest heat gain. With an air mass of 1 the average of the desert species measured was 0.747 cal/cm² min; of the semi-desert species, 0.850; of the single plains species, 0.930; of the eastern and southeastern United States forest animals, 0.948; of the one west European species, 0.989; and, of the tropical rain-forest species, 1.00. The tropical gecko, not directly comparable to the other species because of its nocturnal habits, had a calculated heat gain of 0.859 cal/cm² min. Using these data as a basis, it may be concluded that there is a trend of lower heat gain by the dorsal integuments of diurnal lizards with habitats of increasing aridity and temperature.

The heat gain calculated with an air mass of 5 shows the same correlation of higher values with habitats of increasing moisture and lower temperatures, though the differences between habitat groups are smaller. The difference in heat gain between an air mass of 1 and an air mass of 5 is less for the desert species (0.394 cal) than for the other groups (0.448-0.525 cal). The heat gain under natural conditions would probably approach the values given for an air mass of 5 rather than an air mass of 1 for those species occurring in temperate and tropical areas where cloudiness is common, as opposed to desert and semi-desert areas where cloudiness occurs to an appreciably lesser extent.

These values of calculated heat gain are not a precise description of the heat gain of the animal under natural conditions, but serve as a standard of comparison with some meaning with reference to the thermal relations of the animals. The calculations of the spectral distribution of solar radiation given in Table I were made with certain assumptions and a few arbitrary values. The following conditions were assumed in calclulating these figures: a pressure of one atmosphere, 20 mm of precipitable water, 300 particles of dust per cm³ of air near the ground, an ozone content of 2.8 mm path length at NTP, and a solar constant of 1.94 cal/cm² min. In addition, the segments of the spectrum are rather broad, and a calculation of heat gain using an average of absorptions over these broad segments can only be an approximation. Values of the energy content of each segment of 20 mμ or less of the solar spectrum at sea level would be most useful and would give more precise values for our purposes, but we do not know of any accurate determinations for such short sections of the spectrum.

TABLE II. A Comparison of reflectivity and calculated heat gain of the dorsal skin of lizards from different habitats

Species	Sex	Average percent reflectivity 400-1100 mμ	CALCULATED AVG. HEAT GAIN FROM SOLAR RADIATION IN CAL/CM² MIN.	
			Air mass 1	Air mass 5
Callisaurus draconoides gabbi	♂	31.4	0.734	0.347
Dipsosaurus dorsalis	♀	30.6	0.742	0.351
Phrynosoma platyrhinos calidiarum	♀	35.0	0.695	0.328
Sauromalus o. obesus	♂	23.6	0.818	0.387
			Avg. 0.747	0.353
Crotaphytus c. collaris	♀	18.3	0.874	0.413
	♀	23.8	0.816	0.386
Phrynosoma cornutum	♂	23.2	0.822	0.389
	♀	22.0	0.835	0.395
Sceloporus m. magister	♂	15.4	0.905	0.428
			Avg. 0.850	0.402
Eumeces obsoletus	♀	12.3	0.938	0.444
	♂	14.0	0.921	0.435
			Avg. 0.929	0.440
Anolis c. carolinensis	♂	10.7	0.956	0.452
	♀	11.5	0.947	0.448
Lygosoma laterale	♂	11.5	0.947	0.448
	♀	9.2	0.972	0.460
Ophisaurus ventralis	♀	13.3	0.928	0.439
	♀	16.1	0.898	0.424
Sceloporus u. undulatus	♂	7.5	0.990	0.468
	♀	11.4	0.948	0.448
Sceloporus u. hyacinthinus	♂	12.2	0.940	0.444
	♀	11.4	0.948	0.448
Sceloporus woodi	♂	10.5	0.958	0.453
			Avg. 0.948	0.448
Lacerta muralis	♂	7.7	0.988	0.467
	♀	7.6	0.989	0.468
			Avg. 0.989	0.468
Hemidactylus brookii haitianus	♂	19.7	0.859	0.405
Iguana iguana (juv.)	♀	6.2	1.00	0.475

The reflectances of the ventral skins also show this trend, the desert species having a very high albedo and the forest species a lower albedo. A comparison of the calculated heat gains from solar radiation of the ventral surfaces would not be valid, however. Heat gain by way of the ventral integument is primarily by reflection, conduction and convection from the subtrate and is therefore not due to direct solar radiation. In *Sceloporus* the comparison of ventral reflection is further complicated by the sexual dimorphism in color pattern.

Discussion

The determinations of reflectivities at different wave lengths from the integument is a convenient method of describing the coloration of animals. Coloration as seen by the human eye may be deceptive, superimposed pigments and patterns resulting in blended colors which may appear very similar in 2 different animals when, in fact, they are the result of combined reflectances of completely different dominant wave lengths. In addition, different observers will not "see" the same colors when looking at the same animal. The reflectances are not only due to the presence of pigments, but also to the configuration of the integumentary structures. For these reasons, the method may prove useful as a tool in systematics. It offers a quantitative and objective system for color determinations, with few of the disadvantages found in the use of color standards and color dictionaries, which is always somewhat qualitative and subjective.

Metachromatism of lizards was one of the problems encountered in this study. In those species where color change is due to only 2 environmental factors, such as temperature and illumination, these factors might be controlled and standardized. In those species where the control of metachrosis is complicated by the interaction of several factors, as in *Anolis,* an exact duplication of results would be difficult. The spectral measurement of albedo of a large sample of such a species, however, would give indications of the limits of variability in the population under study. Thus, the disadvantage of poor replication may be an advantage in determining the range of metachrotic changes.

The design of the equipment employed in this study did not permit the use of live animals. It is not known what changes in coloration were brought about in the process of removing the skin from the animals and cleaning it of adhering tissues. There were no changes apparent to the eye, except in *Anolis,* where the color changed from green to a mottling of green and brown. This change occurred at the time of skinning and remained fairly constant during reflectance measurements. As pointed out in the introduction, there were no appreciable changes in albedo during the time of measurements for any of the species examined. Norris (1958) was able to utilize live animals in his study of *Uma,* but the spectrophotometer used recorded only in the visible range of the spectrum.

The use of live animals would also eliminate some of the difficulty in comparing integuments of different transparencies. Undoubtedly, some light passed through the comparatively thin skins of *Hemidactylus, Anolis* and *Lygosoma,* and was reflected by the underlying paper toweling, giving values which may be somewhat different from measurements made on live individuals. On the other hand, the paper toweling was used as a standard underlying layer in all determinations and light reflected through the integument from below was compared on the same basis.

The 4 species and subspecies of *Sceloporus* studied offer an opportunity to compare congeneric lizards of different habitats. The average reflectances of these iguanids are very similar (as are the general shapes of the reflectivity curves (Figs. 2-4)). The only significant difference in dorsal skin albedo is found in the "semi-desert" species, *S. magister,* which had an average reflectance approximately 4.5% higher than the eastern forest forms *S. u. undulatus, S. u. hyacinthinus,* and *S. woodi.* The ventral surface of *magister* was approximately 4% lower than the average of males of the other species in the genus. This lower ventral albedo may have resulted from the relatively darker patches of the ventral surface characteristic of the male *magister,* which was the lowest recorded for all the lizards examined in this study.

Kruger and Kern (1924) estimated that the lizard skin absorbed close to 80% of the incident radiation. Our data show that this estimate was very close. The mean reflectance of the dorsal skins of the 26 individuals examined in this study was approximately 82%, with a range from 65% (*Phrynosoma platyrhinos*) to 94% (*Iguana iguana*).

There is a rather surprising similarly of the reflectivities of the species within any one habitat group, even though the color, texture, and scale size are rather different. For example, the species from the eastern and southeastern forest have average reflectivities of 9.2% to 16.1% for the dorsal skin (Table II), yet the dorsal integuments of *Anolis, Lygosoma, Ophisaurus,* and *Sceloporus* are very different in color and structure when studied visually. Thus, the color and structure of a lizard (and probably most animals) as seen with the human eye gives little indication of the ability of its surface to reflect radiation.

The division of opinion as to whether or not the conformation of reptiles to Gloger's rule is due to the selection advantage of thermoregulatory coloration or to the selection advantage of concealing coloration has been discussed by several investigators (Atsatt 1939, Cott 1939, Klauber 1939, Cole 1943, Cowles and Bogert 1944, Cowles 1958, Norris 1958). These papers may be consulted for discussion and speculations on the adaptive values of reptile coloration.

This argument of protective coloration versus thermoregulatory coloration appears to be unnecessary unless the presence of one function is taken to mean that the other is excluded. Examination of the present evidence indicates that the 2 are synergistic in many cases. For example, in desert reptiles on a light colored substrate, a light coloration would serve to conceal the animal as well as to reduce heat gain. Where the requirements for concealment are greater, selection pressure probably results in the evolution of concealing coloration, taking precedence over thermoregulatory coloration. In cases where thermoregulation is of greater importance, a coloration favoring the metabolic aspects is probably selected for, taking precedence over the requirements of concealment.

SUMMARY

Portions of the dorsal and ventral integuments of 26 individual lizards of 16 different species were used in determinations of skin albedo at 20 mμ intervals over the spectral range from 320-1100 mμ.

The average reflectances of both dorsal and ventral skins were highest in the desert species and decreased, in order, through the semi-desert, plains, eastern and southeastern pine and deciduous forests, European temperate forests, and tropical rain forest species. Reflectivity curves are given for each individual studied.

Calculated average heat gain from direct solar radiation by the dorsal integument in the spectral range of 400-1100 mμ was used as a method of comparing species from different habitats. The average values obtained in cal/cm^2 min and with an optical air mass of 1 were as follows: Desert (0.747), semi-desert (0.850), plains (0.929), eastern and southeastern pine and deciduous forests (0.948), European temperate forests (0.989), and tropical rain forest (1.00). The nocturnal tropical gecko (*Hemidactylus brookii*) had an average calculated heat gain of 0.859 cal/cm^2 min.

The results obtained are discussed in terms of environmental adaptations. Concealing coloration and thermoregulatory coloration appear to be largely synergistic; where the 2 tend to produce opposite effects, the one possessing the greater survival value is probably selected and through evolutionary development becomes the controlling factor.

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THE ECOLOGICAL DISTRIBUTION OF THE DEEP WATER ALGAE OF ENIWETOK ATOLL[1]

INTRODUCTION

Within the Central Pacific, atolls make up the largest percentage of the land mass. Various workers have suggested that many of the physical features of an atoll are due to the growth of its benthic algae. Thus, when a coincidence of interest and technique recently made it possible, a study of the distribution of the benthic algae and the factors effecting this distribution was initiated and carried out at Eniwetok Atoll in 1955-1956 (Fig. 1).

A survey of the literature revealed that few papers are concerned with any phase of the ecological factors affecting the growth and distribution of Central Pacific benthic algae. What information is available (Dawson, 1956, 1957; Taylor, 1950) is hardly more than incident to taxonomic treatments of the littoral and upper infralittoral algae of the specific area visited by the investigator. In particular, information on the lower infralittoral belt (20-65 m) is almost nonexistent, being restricted to bathymetric information on a few specimens secured by dredging, or in shallow areas by skin divers. With the species description, some information concerning algal ecology is available in work done in other parts of the Indo Pacific (Setchell 1926; Boergesen 1913-1953) but quantitative information required for ecological work is completely lacking. Such information is occasionally available from other types of research (Emery, et. al. 1954; Mao 1955; Munk 1954; Von Arx 1954) but is not correlated with any data on the benthic algal communities.

Previous investigations have yielded results interpreted as indicating that growth and distribution of the infralittoral algal species are functions of the quantity of light received (Levring 1947; Taylor 1928). Light is affected by certain factors such as surface turbulence and the amount of suspended material in the water (Poole 1937) but it varies primarily as a function of depth (Whitney 1941). One would thus expect that the decrease in the amount of available light resulting from increased depth would result in changes in both the composition and character of the existing algal communities. These changes could be expressed primarily as a decrease in the number of species with increasing depths, morphological changes of the species with varying depths, and as changes in community composition.

The nature of the substratum can also be expected to play a major role in determining the composition of the communities present. Certain species requiring specific substrata will not exist in a particular community if these substrata are not available. Other species may be able to exist on a variety of substrata.

To a lesser degree, the activities of the benthic fauna may influence the algal community.

MATERIALS AND METHODS

The atolls of the Northern Marshall Islands are particularly favorable for testing these hypotheses by carrying out a special series of observations and collections. Chemical and physical data on Central Pacific atolls and relative accessibility of Eniwetok Atoll, combined with the presence of a well-equipped biological laboratory and an unlimited supply of high pressure air satisfactory for diving, made its selection almost mandatory.

Eniwetok lagoon, with a maximum depth of 65 m, is just within the practical operating limits of compressed air SCUBA (self-contained underwater breathing apparatus). This recently accepted research tool has opened many new areas, particularly the lower infralittoral, for *in situ* investigations. Experiments were conducted along two major approaches. By diving, *in situ* observations and collections of biological and physical information were made. At approximately the same time, standard oceanographic methods were used to collect chemical and physical data on the water mass along the transect.

Eniwetok Atoll itself lies at about 30° 11′ N latitude and 162° 15′ W longitude. The atoll is composed of 30 islets on a reef surrounding an oval shaped lagoon approximately 30 kilometers wide and 40 kilometers long. There are three major passes between the lagoon and the sea: southeast pass between Parry and Japtan islets, 550 m wide with a maximum depth of 58 m; south pass between Eniwetok and Igurin islets, 915 meters wide with a maximum depth of 22 m; and southwest pass, between Giriinien and Rigili islets, 8 kilometers wide with a maximum depth of 3 m. Currents to 2 knots have been reported through southeast pass, and currents to 1 knot through south pass. The mean reported tidal range is .9 m and maximum reported spring tide is 1.6.

Within the lagoon the bottom is relatively flat except for numerous coral patches. Some of these rise within 5 m of the surface and break water at low tide. These patches vary in diameter from 2 to 950 m.

Transect and Stations

The stations were laid out along a lagoon transect reaching from just south of Aniyaanii on the east rim of the atoll to just north of Giriinien on the west rim. This particular transect was selected for several reasons. It was approximately parallel to the prevailing winds and would give the greatest opportunity of noting biological, physical, and chemical gradients. It connected with available offshore lines of sounding, which gave a complete profile of that section of the atoll. The transect occupied approximately the same area investigated by previous workers (Emery et al., 1954) concerned with trans-atoll physical factors; it bisected 2 coral knolls which were respectively 350 and 900 meters in diameter. The terminal station on the west end of the transect was close enough to the base camp to make possible a complete oceanographic run with sufficient time remaining to process the collected samples the same day. Finally, the transect covered a representative bottom profile of the lagoon.

The stations which were selected were marked by buoys to insure repeated dives and collections of chemical and physical data would be made on the same station. Table I and Figure 1 present the station positions (as determined by horizontal sextant fixes) and the station depths.

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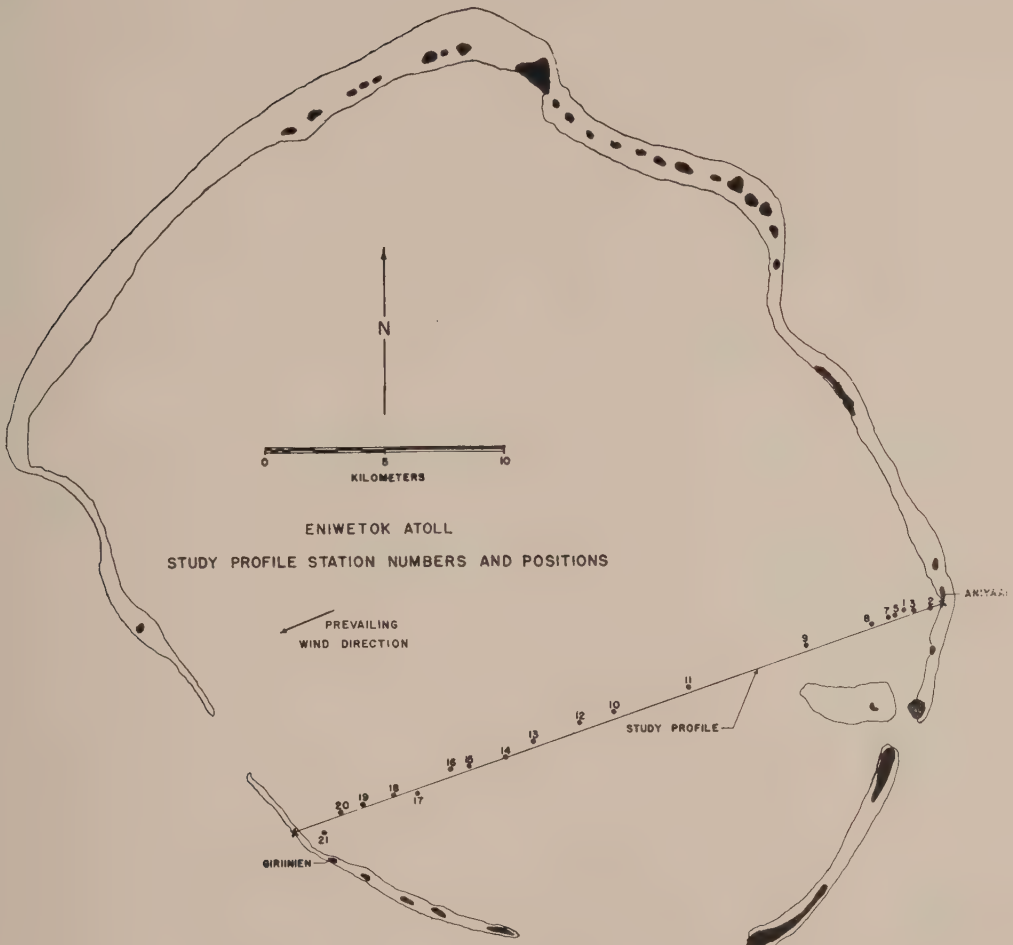


FIG. 1. Map of Eniwetok Atoll showing location of transect stations.

Biological Collecting Methods

A standardized procedure was used for algal collecting at each station. Each diver attached to his diving belt mesh bags containing small plastic sacks. When the diving pair reached bottom on station, one diver would collect the algae on the coral patches. Since the number of species growing on the sand flats was small, the first diver would also collect on the coral patches after he had finished on the sand flats. Several specimens of each of the more conspicuous algae were collected and placed in the mesh bags. Smaller more fragile specimens were placed in plastic bags. In addition to algal specimens, the diver working on the sand flats also collected a sample of the sand substrate.

A 5 gallon bucket with a small crowbar was lowered on station. Just prior to ascent, one diver would break off pieces of coral which were populated with algae and place them in the bucket. The other diver would finish filling the bucket with masses of the dominant algae growing at the station. The mesh collecting bags and the specimens in the bucket were kept moist during the trip back to the laboratory. A physical description of the station and algal communities noted was written *in situ* on plastic slates before surfacing.

At the laboratory, the material was preserved with 10 per cent sea water-formalin, or mounted. Notes and rough field determinations were made at this time. All specimens were shipped back to the University of Hawaii laboratory in Honolulu for final identification and deposit.

RESULTS

Station Descriptions

Oceanographic data on several of the stations (Fig. 1) are presented in Table II.

Station 2 (19 m) was characterized by a fine sand bottom with a moderate eastward gradient approximately 1:6 extending to a sharp gradient break of about 1:1. This break appears to be characteristic of the 8 to 16 m slope of the lagoon rim between islets. The bottom was extremely rough, with mounds of sand and castings covering an estimated 95% of the area. These appeared to be the result of the activities of several different species of burrowing organisms. Except for a few circular patches of Cyanophyta, e.g. *Symploca hydnoides,* and one specimens of *Halimeda monile,* no algae were apparent growing on or attached to large particles in the sand. A few pieces of coral debris were densely popu-

TABLE I. Station positions and depths

Station No.	Depth in meters	Latitude	Longitude
1	5	11°27′56″	162°23′04″
2	19	11°27′56″	162°23′41″
3	28	11°27′52″	162°23′18″
4	9	11°27′46″	162°22′22″
5	41	11°27′47″	162°22′54″
7	46	11°27′45″	162°22′43″
8	49	11°27′34″	162°22′21″
9	53	11°27′06″	162°20′52″
10	6	11°25′39″	162°16′28″
11	62	11°26′11″	162°18′08″
12	63	11°25′24″	162°15′39″
13	62	11°25′02″	162°14′37″
14	9	11°24′36″	162°10′45″
16	57	11°24′23″	162°12′43″
17	51	11°53′23″	162°11′58″
18	52	11°23′49″	162°11′26″
19	43	11°23′24″	162°10′41″
20	35	11°23′24″	162°10′14″
21	19	11°23′08″	162°09′51″

TABLE II. The ranges and means of station oceanographic features

	Temperature °C	Salinity 0/00	Oxygen		PO4 µga/l
			ml/l	% sat.	
Station 2					
range	28.28-28.50	34.42-34.67	1.19-4.18	25.5-89.7	.296-.360
mean	28.34	34.51	3.60	77.3	.331
Station 7					
range	28.30-28.48	34.40-34.58	3.65-4.33	78.3-92.9	.297-.432
mean	28.36	34.50	4.15	89.08	.356
Station 12					
range	28.44-28.64	34.34-34.58	3.70-4.22	79.4-90.6	.378-.509
mean	28.52	34.46	4.06	87.20	.451
Station 16					
range	28.50-28.65	34.22-34.49	4.08-4.60	87.6-98.7	.219-.424
mean	28.56	34.00	4.27	91.62	.313
Station 21					
range	28.54-28.70	34.31-34.47	4.05-4.55	90.8-97.6	.162-.414
mean	28.62	34.41	4.33	92.8	.284

lated with algae. A considerable quantity of algal drift was noted along the base of the 8 to 16 m slope. To the west, staghorn coral appeared at about 25 m and supported a very dense algal population. No major algal dominants were noted, the algal turf on coral being composed of several small populations and an occasional *Halimeda opuntia.*

Station 3 (28 m) was characterized by a dense growth of algae on staghorn coral. The bottom had a shallow 1:10 east gradient. Mounds of sand and castings as noted on the previous station were evident between the staghorn coral and in the clear areas. There were some coral patches growing to a maximum of 1 m diameter and ¾ m in height surmounting low sand mounds. The few clear sand areas were extensively disturbed by burrowing organisms, but where they were relatively undisturbed a circular patch of Cyanophyta or *Halimeda monile* was noted. Both the staghorn coral and the coral patches were densely populated with algae. The algal turf growing on the staghorn coral and on the coral patches had the same gross characteristics.

Station 5 (41 m) had an almost imperceptible eastward gradient to a sand bottom with slightly coarser sand than Station 3. This sand was characterized by having many minute specks (Emery, Tracy, Ladd, 1954). An estimated 15-20% of the bottom area was covered by coral patches ranging in diameter from ¾ to 3 m and growing to a height of 2 m. The sandy flats between coral patches were covered with mounds and castings of the same type as were noted at stations 2 and 3. The few algae that were growing on the sand bottom (*Halimeda monile, Dictyota dichotoma, Dictyota divaricata, Spirulina subsala, Symploca hydnoides*) existed adjacent to the bases of the coral patches. One large Cyanophyte circular patch (½ m in diameter) covered an apparently inactive mound. The coral patches were rather sparsely populated with a light algal turf, a few scattered but conspicuous populants (*Tydemania expeditionis, Halimeda discoida, H. lacunalis, H. opuntia*), and a few scattered and inconspicuous specimens of *Caulerpa racemosa.* All the Halimeda specimens collected were heavily epiphytized.

Station 7 (46 m) had a sand bottom similar to that noted on Station 5. There was no perceptible gradient. An estimated 15% of the bottom area was covered with coral patches up to 3 m in height. These coral patches appeared to surmount sand mounds which made up an estimated average of 25% of the total height. The sandy flats between the coral patches were greatly disturbed with the same type of sand mounds and castings as previously noted. The coral patches were very densely populated with algae but the algae were concentrated on the surface of the patches and did not grow in the crevices as they had on the more shallow stations (2, 3, 5). The coral patches supported a dense growth of various species of *Halimeda* which hosted a smaller number of epiphytes than was found on Station 5. *Halimeda monile* occurred in the rare smooth sand areas between mounds.

Station 8 (49 m) had no apparent gradient to a fine sand bottom characterized by the same black specks noted on Stations 5 and 7. The only coral patch was to the north and about 7 m in diameter and 3 m in height. This particular patch appeared to surmount a sand mound. The sand botttom was flat with none of the mounds noted on the more shallow stations.

The coral patch was densely populated with *Halimeda discoida* and *H. opuntia,* and undergrown with a sparse algal turf. Many large patches of *Lyngbya majuscula,* some to a meter in diameter, covered an estimated 10% of the bottom area, and were intermixed with *Halimeda monile.* Patches up to 2 m in diameter of *Caulerpa sertularioides* were very noticeable These *Caulerpa* patches covered approximately 60% of the sand bottom.

Station 9 (53 m) had an almost imperceptible southward gradient to a fine black specked sand bottom. Two very large coral patches, up to 17 m in diameter and rising to a height of 15 m were visible. These covered an estimated 10% of the visible bottom. Few algae were noted anywhere on the sand flats except around the bases of the coral patches. The patch which was collected had considerable *Dictyota, Halimeda,* and *Tydemania,* and a few scattered, conspicuous *Padina* species. Most of the algae noted were concentrated on the lower 1/5 portion of the coral patch.

Station 10 (6 m) was a large coral patch, approximately 350 m in diameter and rising to within 7 m of the surface. The patch was relatively flat on top but sloping precipitously off to each side. Approximately 80% of the top was covered with various types of coral heads densely populated with algae. A few scattered sand patches composed of coral and *Halimeda* debris occurred between the coral heads. No algae were noted on these patches. The algal flora was characteristically rich in numbers but poor in species. Although usually abundant in shallow areas such as this, no *Asparagopsis* was collected. Various species of *Halimeda* and *Dictyota divaricata* clearly dominated the station from the viewpoint of biomass.

Station 11 (62 m) had no perceptible slope to a fine sand bottom. One large coral patch just visible in the distance was estimated to be 9 m in diameter. A few small coral patches, averaging 1 m in diameter and ⅓ m in height, were found. *Dictyota dichotoma* and *D. divaricata* were the only algae noted growing on the sand. Very noticeable was the absence of *Halimeda monile,* so common on more shallow sand flats. The coral patches were very sparsely populated.

Station 12 (63 m) was similar in general appearance to Station 11. No gradient to the bottom was perceptible, although there was a very slight sand rise to the west. Large coral patches were completely lacking. A few small and scattered, sparsely populated coral heads were noted. On the fine sand flats a few scattered *Dictyopteris repens* specimens were collected, but again no *Halimeda monile* was present.

Station 13 (62 m) was similar to both Stations 11 and 12 in general appearance, with the exception that small coral heads were more numerous. The heads covered an estimated 5% of the bottom area. As on the two previous stations, the coral heads were sparsely populated. *Dictyopteris repens* was the only alga collected on the sand flats.

Station 14 (9 m) was a large coral patch coming to within 9 m of the surface. It was similar in appearance to Station 10 but was approximately 950 m in diameter. The top was almost completely covered with coral heads averaging 1 x 1 m. An occasional coral head exceeded 3 m in height. The sandy areas between coral heads did not support any algae. The coral itself was densely populated, primarily with *Asparagopsis taxiformis, Dictyota dichotoma* and *D. divaricata.* Within the community a few scattered *Halimeda* and other genera were evident. As at Station 10, the community was rich in numbers but poor in species.

Station 16 (57 m) lacked a gradient to a rolling sandy bottom characterized by many small sand hummocks. Some of these hummocks were topped with low coral patches. This station differed markedly from Stations 11, 12 and 13 which occurred at similar depths. The coral patches were relatively densely populated, dominated by *Tydemania expeditionis. Dictyopteris repens* was quite common, growing attached to coarse particles in the sand.

Station 17 (51 m) had the same rolling bottom characteristic of Station 16. The coral patches were relatively densely populated with numerous algal species. The dominant species as to bulk was difficult to determine. Both *Tydemania expeditionis* and various species of *Halimeda* occurred in approximately the same abundance. This was the deepest station on the west end of the transect at which *Halimeda monile* and the Cyanophyta patches appeared on the sand flats.

Station 18 (52 m) was similar in topographic appearance to both Station 16 and Station 17. The algal community differed only in the presence of patches of *Caulerpa racemosa* var. *peltata* growing on the sand flats between coral heads.

Station 19 (43 m) was located in a valley between 3 sand hummocks topped by coral patches averaging 7 m in diameter and 3 m in height. These coral growths differed from those at similar depths on the eastern end of the transect by a larger percentage of the total height of the sand-coral unit being sand. The sand area between these coral hills was extensively populated with *Halimeda monile* evenly spaced on approximately 1 m centers. A few small patches of *Caulerpa acuta* were intermixed among the *Halimeda.* Scattered Cyanophyta communities were noted. The coral patches were densely overgrown with *Halimeda fragilis. Tydemania expeditionis* secondarily dominated the community. In addition to a sparse algal understory on the coral patches, an occasional dense patch of a single species was noted.

Station 20 (35 m) had a very irregular bottom with an apparent 1:8 westward gradient. Many small rises, dips and hummocks disrupted the bottom, but these did not seem to result from the activities of burrowing organisms characteristic of similar depths on the eastern end of the transect. Some of the sand hummocks were topped with coral patches rising to an estimated 2 m, and occasionally reaching 6 m in diameter. These coral patches were densely populated with minute growths of many different algae. *Halimeda* again dominated in bulk both the coral patches and the sand flats.

Station 21 (19 m) had a fine sand bottom with an estimated 1:8 westward gradient. At about 18 m a sharp, estimated 1:1 slope led up to a depth of 6 m. This slope was similar to that noted on the eastern end of the transect. Considerable drift was evident at the base of this slope. Staghorn coral and coral rubble, densely populated with an algal turf, lay scattered about the station. *Halimeda* was evident growing upon an occasional small coral head. On the sand bottom, *Halimeda monile* and scattered *Dictyopteris* and *Dictyota* were intermixed with an occasional patch of Cyanophyta.

Systematic List

This systematic list is primarily a record of the species determined during this study. The species are listed in systematic order with information on substrata, stations, and depth. Whenever possible useful taxonomic literature has been cited, particularly when it contained applicable illustrations. No special effort was made to examine or cite the original species description except when the publication was available locally. Whenever possible controversial problems of nomenclature were avoided. Those species marked "**" have not previously been reported from the Marshall Islands. The observed local distribution is reported for each species.

CYANOPHYTA

Hormorthamnion enteromorphoides Grunow; ex Bornet & Flahault; Dawson 1954; 379, fig. 3n; Taylor 1950: 105. Very rare, on sand. Sta. 3, depth 28 m.

Scytonema polysystum Bornet & Flahault. Very rare, on sand, Sta. 3, depth 28 m.

Spirulina subsala Oersted ex Gomont 1893. Very rare, on sand. Sta. 3, 5, depths 28-41 m.

Lyngbya majuscula (Dillwyn) Harvey ex Gomont; Taylor 1950: 111. Very rare, forming circular colonies on sand, or on coral. Sta. 8, 20, depths 35-49 m.

Lyngbya sordida f. *bostrychicola* (Crouan) Bornet. Very rare, on sand. Sta. 3, depth 28 m. No. 516.

Symploca hypnoides Kützing: Dawson 1954; 380, figs. 3o. Abundant, on sand or on coral. Sta. 2, 5, 7, 12, 13, 17, 19, depths 19-63 m.

Symploca laete-viridis Bornet. Very rare, on coral. Sta. 7, depth 46 m.

Hydrocoleum comoides (Harvey) Gomont. Very rare, on sand. Sta. 21, depth 19 m.

Hydrocoleum glutinosum (C. Agardh) Bornet. Very rare, on coral. Sta. 17, depth 51 m. No. 945 b.

CHLOROPHYTA

Valonia aegagropila C. Agardh; Egerod 1952: 348, pl. 29, fig. b; Dawson 1956; 28; Taylor 1950: 41. Very rare, epiphytic on *Halimeda,* or on coral. Sta. 5, 17, depths 41-51m.

Valonia utricularis (Roth) C. Agardh; Dawson 1956: 28 fig. 3. Very rare, epiphytic on *Halimeda,* or on coral. Sta. 13, 16, depths 57-62 m.

Valonia ventricosa J. Agardh; Egerod 1952: 348, pl. 29, fig. 8a, Dawson 1954: 388, fig. 8e, Dawson 1956: 28. Very rare, on coral. St. 5, 9, depths 41-53 m.

Cladophoropsis gracillima Dawson; Dawson 1950a; 149, fig. 12-13; Dawson 1956: 30, fig. 7a, b. Very rare, on coral. Sta. 2, depth 19 m.

Cladophoropsis sundanensis Reinbold; Dawson 1956; 30, fig. 8; Dawson, Aleem & Halstead 1955; 10. Very rare, epiphytic on *Halimeda.* Sta. 2, depth 19 m.

***Derbesis neglecta* Berthold; Boergesen 1925: 105, fig. 43-44. Very rare, on coral. Sta. 7, depth 46 m.

Boodlea composita (Harvey) Brand; Taylor 1950: 44; Dawson 1954: 390, fig. 9c, d; Dawson 1956: 30. Very rare, on coral. Sta. 3, depth 28 m.

***Cladophora albida* (Hudson) Kützing; Kutzing Tab. Phyc. 4. pl. 15, fig. b; Dawson 1954: 386, fig. 7f, g. Very rare, on coral. Sta. 20, depth 35 m.

***Cladophora gracilis* (Griffiths) Kützing: 4, p. 23, fig. 2; Taylor 1928: 63, pl. 4, fig. 1. Very rare, on coral. Sta. 20, depth 35 m.

Cladophora socialis Kützing; Kützing Tab. Phyc. 4, pl. 71; Dawson 1956: 34. Very rare, on coral. Sta. 11, depth 62 m.

Bryopsis pennata Lamouroux; Egerod 1952; 370, fig. 7; Dawson 1954: 393, fig. 11b; Dawson 1956: 34. Very rare, on coral. Sta. 21, depth 19 m.

Caulerpa acuta (Yamada) Yamada; Dawson 1957; *Caulerpa filicoides* Yamada 1936: 135, pl. 30, fig. 2; *Caulerpa verticilata* f. *acuta* Yamada 1934: 63, fig. 32. Common, very rarely epiphytic on *Halimeda,* usually on coral. Sta. 11, 12, 14, 16, 19, depth 9-63 m.

Caulerpa brachypus Harvey; Taylor 1950: 56, pl. 29, fig. 2. Very rare, on coral. Sta. 12, depth 63 m.

Caulerpa peltata Lamouroux; Collins & Harvey 1917: 65; Caulerpa peltata (Turner) Lamoroux, Taylor 1928: 100, p. 12, fig. 9, pl. 13, fig. 13; Taylor 1950: 65. Very rare, on coral. Sta. 16, depth 57 m.

Caulerpa racemosa (Forskal) J. Agardh, var., *clavifera* (Turner) Weber van Bosse; Weber van Bosse 1898: 362, pl. 33, figs. 1-5; Taylor 1950: 62. Rare, on coral. Sta. 12, 14, 17, depths 9-63 m.

Caulerpa racemosa var. *macrophysa* (Kutzing) Taylor; Taylor 1928: 101, pl. 12, fig. 3, pl. 13, fig. 9; Taylor 1950: 63; Dawson 1954: 393, fig. 10c; Dawson 1956; 35. Very rare, on coral or on *Halimeda* fragments in sand. Sta. 7, 19, depths 43-46 m.

Caulerpa racemosa var. *peltata* (Lamouroux) Eubank; Dawson 1956: 35, fig. 16b. Common, on coral. Sta. 5, 14, 17, 18, 20, depths 9-52 m.

Caulerpa serrulata (Forsskal) J. Agardh; Dawson 1954: 393, fig. 10a; Dawson 1956: 38; Taylor 1950: 57. Rare, forming stolon system over sand substrata. Sta. 8, 11, 16, 18, depths 49-62 m.

Caulerpa sertularioides (Gmelin) Howe; Boergesen 1913: 133, fig. 106; Dawson 1956: 38, fig. 22; Taylor 1928: 103, pl. 13, fig. 5. Very rare, forming stolon system over sand substrata. Sta. 8, 16, depths 49-57 m.

Caulerpa verticillata J. Agardh; Dawson 1954: 392, fig. 10b; Dawson 1956: 37: Taylor 1928: 103, pl. 12, fig. 7, pl. 13, fig. 2; Taylor 1950: 54. Very rare, on coral or attached to large particles in sand. Sta. 8, 20, depths 35-49 m.

Caulerpa vickersiae Boergesen; Boergesen 1913; 119, fig. 94; Dawson 1956: 35, fig. 18. Very rare, epiphytic on *Halimeda* or on coral. Sta. 17, 20, depths 35-51 m.

Caulerpa webbiana Montagne; Boergesen 1913: 125, fig. 99; Boergesen 1925: 109; Boergesen 1940: 45. Very rare, on coral. Sta. 8, depth 49 m.

Pseudochlorodesmis furcellata (Zanardini) Boergesen; Boergesen 1925: 78, figs. 30-34; Dawson 1954: 395, fig. 11c; Dawson 1956: 39; Hamel 1931: 401, fig. 21b. Very rare, intermixed wtih dense-*Asparagopsis,* or on coral. Sta. 2, 14, depths 9-19 m.

***Avrainvillea nigricans* Decaisne; Boergesen 1913: 84, fig. 69; Gepp 1911: 23, fig. 78-80; Taylor 1928: 77, pl. 8, fig. 10, pl. 11, fig. 8; Vickers 1908: 23, pl. 30. Very rare, on coral. Sta. 11, depth 62 m.

Acetabularia moebii Solms-Laubach; Boergesen 1940: 44; Dawson 1954; 397, fig. 13; Dawson 1957; Egerod 1952: 411, fig. 231. Very rare, on coral. Sta. 20, depth 35 m.

Tydemania expeditionis Weber van Bosse; Dawson 1956: 41; Srinivasan 1954: 247-255; Taylor 1950; 73, pl. 38, fig. 1; Weber van Bosse 1901: 139; Weber van Bosse 1913: 66, fig. 153, 154. Very abundant, both in glomeruliferous and flabelloid forms, on coral. Sta. 5, 8, 9, 12, 16, 17, 18, 19, depths 9-63 m.

Udotea indica A. & E. S. Gepp; A. & E. S. Gepp 1911: 121, fig. 13, 14, 52, 53; Taylor 1950: 74, pl. 36, fig. 2. Very rare, on coral. Sta. 20, 21, depths 19-35 m.

Udotea javensis (Montagne) A. & E. S. Gepp; Dawson 1954; 395, fig. 13b, c; Dawson 1956: 40; Taylor 1950: 73. Rare, on coral. Sta. 2, 7, 17, 20, depths 19-51 m.

Udotea orientalis A. & E. S. Gepp; A. & E. S. Gepp 1911: 119, fig. 1, 4, 47, 48; Taylor 1950: 74, pl. 38, fig. 2. Very rare, on coral. Sta. 21, depth 19 m.

Codium geppii O. C. Schmidt; Boergesen 1936: 68, fig. 3; *Boergesen* 1946: 49, fig. 195-199; Dawson 1954: 395, fig. 13k; Dawson 1956: 39, fig. 26. Very rare, on coral. Sta. 8, depth 49 m.

Halimeda discoida Decaisne; Boergesen 1913: 106; Howe 1907: 495; Taylor 1950: 85, pl. 45, fig. 1; Taylor 1928: 82, pl. 10, fig. 17, pl. 11, fig. 23. Common, on coral. Sta. 5, 7, 8, 9, 17, 18, depths 41-53 m.

Halimeda fragilis Taylor; Taylor 1950: 88, pl. 48, fig. 2. Abundant, on coral. Sta. 9, 11, 12, 14, 16, 17, 18, 19, 20, 21.

Halimeda gracilis Harvey; Barton 1901: 22; Boergesen 1913: 108; Dawson 1954: 396, fig. 13f; Dawson 1956: 42. Very rare, on coral. Sta. 16, depth 57 m.

Halimeda lacunalis Taylor; Taylor 1950: 91, pl. 51. Common, on coral. Sta. 5, 7, 11, 12, 17, depths 41-63 m.

Halimeda monile (Ellis & Solander) Lamouroux; Dawson 1956: 41; Taylor 1950: 93, pl. 50, fig. 1. Abundant, on sand flats between coral knolls. Sta. 2, 5, 7, 17, 18, 19, 20, 21, depths 19-51 m.

Halimeda opuntia (Linnaeus) Lamouroux; Barton 1901: 18, fig. 19-27; Boergesen 1913: 108; Dawson 1954: 395, fig. 12; Dawson 1956: 41; Taylor 1950: 80, pl. 39, fig. 1. Abundant, on coral. Sta. 2, 5, 7, 8, 9, 12, 14, 16, 17, 18, 20, 21, depths 9-63 m.

***Halimeda opuntia* f. *elongata* (Barton) Barton; Barton

1901: 21, fig. 24, Taylor 1950: 82, pl. 41. Rare, on coral, Sta. 9, 19, 20, depths 19-53 m.

Halimeda opuntia f. *hederacea* Barton; Barton 1901: 21, fig. 23; Taylor 1950: 81, pl. 40, fig. 1. Rare, on coral. Sta. 11, 16, 17, depths 51-62 m.

Halimeda opuntia f. *minima* Taylor; Taylor 1950: 82, pl. 39, fig. 2. Very rare, on coral. Sta. 12, depth 62 m.

Halimeda taenicola Taylor; Taylor 1950: 86, pl. 46, fig. 1; Dawson 1956: 42. Very rare, on coral. Sta. 9, depth 53 m.

***Halimeda tridens* (Ellis & Solander) Lamouroux; Taylor 1928: 84, pl. 10, fig. 14. Very rare, on coral. Sta. 12, 19, depths 43-63 m.

PHAEOPHYTA

Sphacelaria furcigera Kützing; Boergesen 1941: 46, fig. 21; Dawson 1954: 400, fig. 14h; Dawson 1956: 44; Kützing, Tab. Phyc. 5, pl. 90, fig. 2. Very rare, epiphytic on *Halimeda*. Sta. 20, depth 35 m.

Pocockiella variegata (Lamouroux) Papenfuss; Dawson 1954: 400, fig. 14k; Dawson 1956: 44; Papenfuss 1947: 467, figs. 1-14. Rare, epiphytic on *Halimeda*, or more commonly on coral. Sta. 2, 17, 19, 20, depths 19 to 51 m.

***Dictyota cervicornis* Kützing; Kützing Tab. Phyc. 9, pl. 24, fig. 2; Taylor 1928: 118, pl. 16, fig. 17. Very rare, on coral. Sta. 17, depth 51 m.

***Dictyota dichotoma* (Hudson) Lamouroux; Dawson 1954: 401, fig. 15; Okamura, Icones 3: 39, pls. 111-113; Dawson 1950a: 90. Common, epiphytic on *Halimeda*, on coral, or attached to coarse particles in sand. Sta. 5, 11, 12, 14, 18, 20, 21, depths 19-63 m.

Dictyota divaricata Lamouroux; Taylor 1928: 120, pl. 16, figs. 6-9; Taylor 1950: 101. Very common, occasionally epiphytic on *Halimeda*, rarely epiphytic on *Tydemania*, on coral, most commonly attached to coarse particles in sand. Sta. 2, 5, 7, 8, 9, 11, 14, 16, 17, 19, 21, depths 19-63 m.

Dictyopteris repens (Okamura) Boergesen; Dawson 1956: 44, fig. 34. Abundant, rarely epiphytic on *Halimeda* or on coral, most attached to coarse particles in sand. Sta. 2, 5, 7, 8, 9, 11, 12, 17, 18, 19, 20, 21.

Padina commersonii Bory; Boergesen 1930; 170; Dawson 1954: 401, fig. 17; Dawson 1956: 44; Taylor 1950: 100, pl. 54, fig. 1; Weber-van Bosse 1913: 178, fig. 51. Common, very rarely epiphytic on *Tydemania*, usually on coral. Sta. 7, 9, 16, 17, 20, depths 35-53 m.

RHODOPHYTA

***Rosenvingea orientalis* (J. Agardh) Boergesen; Boergesen 1930b: 168; Dawson 1954: 404, fig. 19a. Very rare, epiphytic on *Halimeda*. Sta. 20, depth 35 m.

***Spatoglossum schroederi* (Mertens) J. Agardh; Collins & Hervey 1917: 84; Taylor 1928: 124, pl. 17, fig. 2. Very rare, on coral. Sta. 16, depth 53 m.

Acrochaetium robustum Boergesen; Abbott 1946: 203, fig. 4; Boergesen 1915: 40 fig. 38-40; Dawson 1954: 414, fig. 25j, k; Tseng 1945. 158 pl. 1; fig. 2-4. Very rare, on coral. Sta. 7, depth 46 m.

Asparagopsis taxiformis (Delile) Collins & Hervey; Boergesen 1942: 59; Collins & Hervey 1917: 117. Rare, but locally in shallow areas quite abundant. Sta. 12, 14, depths 9-63 m.

Falkenbergia hillebrandii (Bornet) Falkenberg; sporophyte generation of *Asparagopsis taxiformis* (Delile) Collins & Hervey; Boergesen 1913; 311, fig. 332-333; Dawson 1954: 414, fig. 251; Dawson 1956: 45; Falkenberg 1901: 689; Taylor 1928: 175, pl. 25, fig. 4-5. Very rare, epiphytic on *Halimeda*. Sta. 12, depth 63 m.

Galaxura filamentosa Chou; Chou 1945: 39, pl. 1, fig. 1-6, pl. 6, fig. 1; Dawson 1956: 51, pl. 19, fig. 2; Dawson 1954: 419, fig. 30a; Dawson 1956: 46. Very rare, on coral. Sta. 12, depth 63 m.

Gelidiopsis intricata (C. Agardh) Vickers; Dawson 1954: 423, fig. 34a-d; Dawson 1956: 46; Yamada & Tanaka 1938: 74, fig. 6a-c. Very rare, on coral. Sta. 2, depth 19m.

Jania capillacea Harvey; Boergesen 1915: 198, fig. 188; Dawson 1954; 432, fig 41a, b; Dawson 1956: 49; Taylor 1928: 206, pl. 29, fig. 2, 10. Rare, epiphytic on *Halimeda*, or on coral. Sta. 2, 12, 21, depths 19-63 m.

Jania decussato-dichotoma (Yendo) Yendo; Dawson 1956: 49, fig. 44; Yendo 1905: 37. Very rare, on coral. Sta. 18, depth 52 m.

Hypnea esperi Bory; Dawson 1954: 436, fig. 46h-j; Dawson 1956: 51. Very rare, epiphytic on *Halimeda*. Sta. 7, depth 46 m.

Botryocladia skottsbergii (Boergesen) Levring; Dawson 1956: 52, fig. 48. Common, on coral. Sta. 5, 12, 14, 16, 17, 18, depths 9-63 m.

Champia parvula (C. Agardh) Harvey; Boergesen 1915: 407, fig. 392, 393; Dawson 1954: 443, fig. 52c; Dawson 1956: 51; Taylor 1928: 158, pl. 24, fig. 3. Very common, epiphytic on *Halimeda* and on coral. Sta. 2, 5, 8, 12, 17, 18, 20, 21, depths 19-63 m.

Rhodymenia anastomosans Weber-van Bosse; Dawson 1956: 52, fig. 49. Rare, repentent on coral. Sta. 12, 16, 17, depths 51-63 m.

Antithamnion lherminiera (Crouan & Crouan) Nasr; Dawson 1956: 53, fig. 51; Nasr 1941: 66, fig. 9, 10. Common, epiphytic on *Halimeda*. Sta. 2, 5, 7, 12, 17, depths 19-63 m.

Spermothamnion saccorhiza (Setchell & Gardner) Feldmann-Mazoyer; Dawson 1956: 56, fig. 57. Very rare, epiphytic on *Halimeda*. Sta. 7, depth 46 m.

***Mesothamnion caribaeum* Boergesen; Boergesen 1915: 208, fig. 194-200; Dawson 1954: 444, fig. 54a, b. Very rare, epiphytic on *Halimeda*. Sta. 21, depth 19 m.

Griffithsia tenuis C. Agardh; Boergesen 1915: 462, fig. 423; Abbott 1946: 441, pl. 3, fig. 1-7; Dawson 1954: 450, fig. 56e; Dawson 1956: 56. Very rare, epiphytic on *Udotea* or on coral. Sta. 2, 21, depths 19 m.

***Haloplegma duperreyi* Montagne; Kützing Tab. Phyc. 12, pl. 62; Boergesen 1945: 11, fig. 3. Very rare, epiphytic on *Halimeda*. Sta. 20, depth 35 m.

Ceramium graccillimum var. *byssoideum* (Harvey) G. Mazoyer; Dawson 1954: 448, fig. 55e, f; Dawson 1956: 53. Very rare, epiphytic on *Halimeda* and *Dictyota*. Sta. 7, 17, depths 46-63 m.

Ceramium mazathanense Dawson; Dawson 1950b: 130, pl. 2, fig. 15, 14; Dawson 1954: 448, fig. 55g-j; Dawson 1956: 53. Very rare, epiphytic on *Halimeda* or on coral. Sta. 20, 21, depths 19-35 m.

Centroceras clavulatum (C. Agardh) Montagne; Dawson 1954: 446, fig. 54b; Dawson 1956: 55; Smith 1944: 328, pl. 84, fig. 5, 6; Taylor 1950: 139. Very rare, epiphytic on *Halimeda*. Sta. 20, depth 35 m.

Spyridia filamentosa (Wulfen) Harvey; Boergesen 1915: 233, fig. 222-226; Dawson 1954: 444, fig. 54i; Dawson 1956: 56; Taylor 1928: 197, pl. 28, fig. 4, 18; Taylor 1950: 139.

Hypoglossum minimum Yamada; Dawson 1957; Yamada 1936; 138, fig. 2a-d. Common, very rarely on coral, usually epiphytic on *Halimeda*. Sta. 5, 7, 12, 17, depths 41-63 m. 934.

***Dasya corymbifera* J. Agardh; Boergesen 1915: 323; Taylor 1928: 172; Collins & Harvey 1917: 131. Very rare, epiphytic on *Halimeda*. Sta. 9, depth 53 m.

Dasya iyengarii Boergesen; Boergesen 1937: 345, fig. 16, 17; Dawson 1957. Very rare, epiphytic on *Halimeda*. Sta. 17, depth 51 m.

Dasya mollis Harvey; Harvey 1853: 62; Boergesen 1915: 317, fig. 321; Dawson 1957; Taylor 1928: 173, pl. 26, fig. 13. Rare, epiphytic on *Dictyopteris*, or more commonly epiphytic on *Halimeda*. Sta. 12, 17, 18, depths 52-63 m.

***Heterosiphoni wurdemanii* (Bailey) Falkenberg var. *laxa* Boergesen: Boergesen 1915: 324, fig. 327. Rare, very rarely epiphytic on *Dictyopteris*, usually epiphytic on *Halimeda*. Sta. 17, 18, 19, depths 43-51 m.

Heterosiphonia wurdemanni (Bailey) Falkenberg var. *wurdemanni;* Falkenberg 1901: 638, pl. 16, fig. 11; Boergesen 1915: 324, fig. 326; Taylor 1950: 140. Common, very rarely on coral, usually epiphytic on *Halimeda*. Sta. 2, 5, 17, 20, 21, depths 19-51 m.

Polysiphonia subtilissima Montagne; Dawson 1954: 454, fig. 60c; Dawson 1956: 58; Taylor 1928: 185, pl. 25, fig. 14, pl. 26, fig. 14; Tseng 1944: 70, pl. 1. Very rare, epiphytic on *Halimeda*. Sta. 20. depth 35 m.

Polysiphonia tongatensis Harvey; Dawson 1954: 454, Fig. 60d, e; Dawson 1956: 57; Hollenberg 1942a: 784; Kützing Tab. Phyc. 14, pl. 41. Very rare, on coral. Sta. 2, 21, depths 19 m.

Tolypiocladia calodictyon (Harvey) Silva; Dawson 1956: 58, fig. 62. Rare, epiphytic on *Asparagopsis, Halimeda*, or on coral. Sta. 14, 20, 21, depths 9-35m .

Lophosiphonia obscura (C. Agardh) Falkenberg; Dawson 1957; Falkenberg 1901: 500; Boergesen 1915: 294, fig. 292-294; Dawson 1954: 451, fig. 58d, e. Rare, intermixed with *Bryopsis* on coral. Sta. 21, depth 19 m.

***Lophosiphonia villum* (J. Agardh) Setchell & Gardner; Dawson 1954: 541, fig. 58f, g; Hollenberg 1942b: 535, fig. 11-13; Setchell & Gardner 1903: 329; Smith 1944: 364, pl. 94, fig. 1. Very rare, epiphytic on *Halimeda*. Sta. 2, 20, depths 19-35 m.

***Chondria baileyana* (Montagne) Harvey; Dawson 1954: 460, fig. 62a; Harvey 1853: 20, pl. 18a; Taylor 1937: 358, pl. 55, fig. 4. Rare, epiphytic on *Halimeda*, on coral or on coarse particles in sand. Sta. 7, 11, 12, 14, depths 9-63 m.

Chondria repens Boergesen; Boergesen 1924: 300, fig. 40; Dawson 1954: 460, fig. 62d, e; Dawson 1956: 60. Common, very rarely on coral, usually epiphytic on *Halimeda*. Sta. 2, 5, 14, 17, 20, depths 9-51 m.

***Crouania attenuata* (Bonnemaison) J. Agardh; Okamura Icon. 5: 124, p. 235, fig. 15-21; Taylor 1928: 193, pl. 27, fig. 7-9, pl. 32, fig. 9. Very rare, epiphytic on *Halimeda*. Sta. 2, 21, depths 19 m.

DISCUSSION

General Remarks

Subsequent analysis of data and specimens gathered on field trips showed that the main contribution is an account of the lower infralittoral benthic algae species and their distribution in the deeper water of Eniwetok lagoon.

The original study was based on the assumption that the abundance of benthic algae would be such that a representative quantitative sample could be collected during the diving time available on station. The initial station surveys showed that the area necessary for a representative quadrat would have to be increased a hundredfold. There was not sufficient time available during a dive to collect such a quadrat. Thus this quantitative phase of the study was modified.

Conclusions on the relative abundance of algal dominants were based on comparative observations made while diving at the various stations. Since these observations were actually written while the author was underwater on the station, it is felt that they are reasonably reliable.

The following discussion considers the hypotheses concerning the distribution of the lower infralittoral benthic algae in the same order as they were enumerated in the introduction to this paper.

Algal Distribution

Previous workers in the Marshall Islands (Dawson 1956, 1957; Taylor 1950) have reported a total of 271 species and varieties of algae. Of these, the majority were collected in the littoral and upper infralittoral belts. During this investigation, 413 collections of 95 species and varieties were made. Eighteen per cent of the 90 species collected were unreported for the Marshall Islands. With but one exception, *Dictyota dichotoma*, these unreported species were noted locally as rare or very rare forms, usually collected at depths greater than 35 m.

The bathymetric distribution of the deeper water Eniwetok algae is shown in Figures 2 and 3.

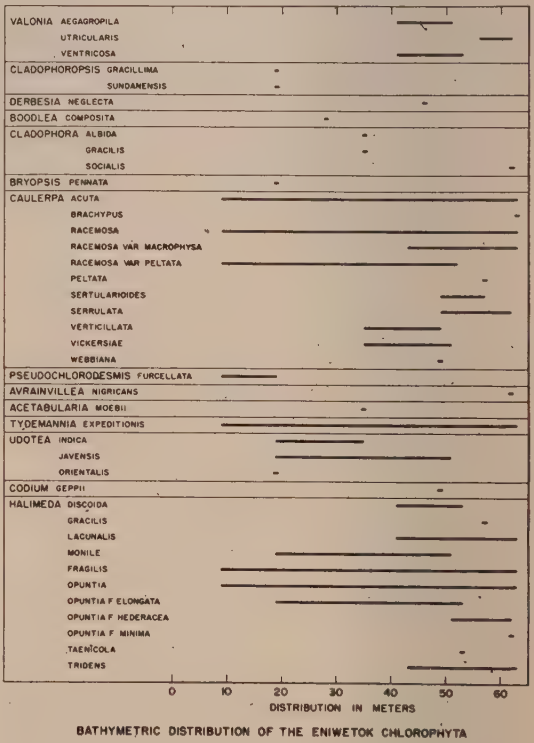
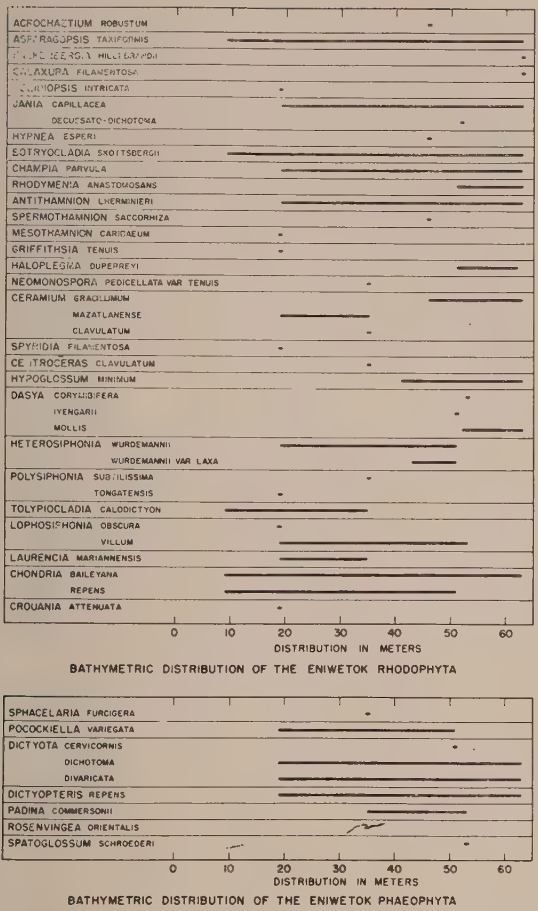


FIG. 2. The bathymetric distribution of Eniwetok Chlorophyta.

Among the Chlorophyta, 3 genera had eubenthic species, but even among these genera, the majority of species were stenobenthic to some degree. The most common genus, occurring on all stations, was *Halimeda*. Two species, *H. fragilis* and *H. opuntia* occurred at all



BATHYMETRIC DISTRIBUTION OF THE ENIWETOK RHODOPHYTA

BATHYMETRIC DISTRIBUTION OF THE ENIWETOK PHAEOPHYTA

FIG. 3. The bathymetric distribution of Eniwetok Rhodophyta and Phaeophyta.

depths. Eight of the 10 species of *Halimeda* occurred primarily between the 41 and 62 m stations. This would support previous reports that this genus is most common and luxuriantly developed at the deeper levels.

Of interest are the data and observations that, with the exception of *H. monile, Halimeda* species were noted and collected only on the sides and tops of the coral patches. The general impression held by many workers, apparently based on the abundant *Halimeda* usually gathered during any lagoon dredging operation, is that this genus forms large, dense patches on the lagoon bottom. This view was not supported by any of the data gathered or observations made during this study.

The second genus to be noted, *Caulerpa*, also had three eubenthic species; 7 of the 11 species collected were concentrated between the 35 and 57 m stations.

Tydemannia was the third genus having eubenthic species. This previously rarely reported alga was abundant at the majority of stations, both in the glomeruliferous and the flabelloid form. In number and in mass this species was an important constituent of most station communities.

Among the apparently stenobenthic Chlorophyta collected, the three species of *Valonia* were obvious. Many separate specimens were collected, but only at stations with depths in excess of 41 meters. These same species were collected as littoral and upper infralittoral species by both Dawson and Taylor.

Occasional single collections of Chlorophyta were made that were restricted to deeper stations A single, very fine, well developed specimen of *Avrainvillea nigricans* was collected at the 63 m station This has been reported previously as a deep water species in the Danish West Indies by Boergesen (1913) *Caulerpa webbiana,* collected only once at 49 m, has often been reported from the Indo-Pacific as occurring in the 30-60 m depths. Several species of *Halimeda,* reported by Taylor to occur in deep water, were collected.

The bathymetric distribution of the Phaeophyta, Fig. 3, is characterized by the eubenthic genera *Dictyopteris* and *Dictyota.* Three of the 4 species in these genera were collected at most stations. Collections of *Pocockiella variegata* were made only at stations with depths between 35 and 51 m. Since this species was collected only as an epiphyte on the caulescent basal portion of *H. monile,* whose lower limit was also the 51 m station, it would appear that the range restriction of *Pocockiella* results from lack of a suitable substratum rather than from depth. *Padina commersonii,* a species common on the adjacent reef flats, was collected only between the 35-53 m stations. On these stations, the specimens were quite conspicuous though usually few in number and they appeared to be well developed members of the communities. Of note is the apparent absence of *Sargassum* which seems to support other worker's (Doty 1954) views regarding the exclusiveness of the range of this genus.

One specimen of *Spatoglossum schroederi* was collected at the 53 m station. This species is apparently unreported for the tropical Indo-Pacific. It is a small, occasional deep-water species in this area and this is probably the reason it has not been collected previously. It is commonly reported as a littoral and lower infralittoral species in the Atlantic.

As shown in Fig. 3, many of the Rhodophyta were collected only at the deeper stations. Certain genera, such as *Botryocladia, Antithamnion, Jania* and *Chondria* occurred throughout the entire depth range. Others such as *Tolypiocladia, Laurencia* and *Lophosiphonia* were sharply restricted as to lower limits. *Galaxura, Falkenbergia* (the sporophyte generation of *Asparagopsis*), *Haloplegma* and *Hypoglossum* were collected only on deep water stations. Certain species such as *Cerami-*

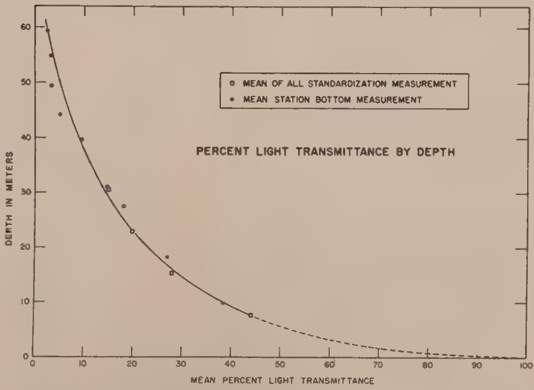


FIG. 4. The mean per cent of surface light transmittance at various station depths.

um, quite common in the reef flat turf, were not collected on any stations more shallow than 46 m.

The Rhodophyta, commonly thought of as distinctively deep water algae, were never represented by any species which could be considered as biomass-important members of the deep water communities. Numerous small, single specimens of Rhodophyta occurred as epiphytes on *Halimeda*, or as a very sparse, minute algal turf on coral patches (see systematic list). The majority of stations were dominated in bulk by *Halimeda* species, and when present, *Dictyopteris* and *Dictyota* dominated numerically. The Chlorophyta often reached 15-20 cm in height, whereas members of the Rhodophyta rarely exceeded 2 cm and Phaeophyta 6 cm. *Tydemannia*, as an understory, secondarily dominated most of the communities in which it occurred, although on a few stations *Dictyota* and *Dictyopteris* exceeded it in bulk as well as in numbers.

The lack of a specifically distinct deep water algal flora, combined with the fact that a relatively large percentage of the species collected also occurred as littoral and upper infralittoral community members, leads to a general conclusion.

The presence, or the absence, of a species on a particular station should indicate the range of chemical and physical factors under which it can grow. The degree of dominance and luxuriance may give some indication of the most favorable range of conditions.

It is hypothesized that the littoral and upper infralittoral community members release reproductive bodies which, in effect, "seed" the entire transect substratum. There is sufficient unoccupied substratum on all stations for any reproductive bodies capable of developing under station conditions to do so.

From the species collected, it would seem that about 35% of these community members release reproductive bodies that are able to develop and grow under the conditions present at the various stations. The relative size and infertile state of many of the specimens which were collected suggests that they are on the borderline of factors controlling their growth, and do little more than survive. The species that are able to grow efficiently under these conditions come to dominate the community in number or in mass.

Distribution of the Algae as Related to Trans-lagoon Chemical and Physical Gradients

In general the oceanographic features of the lagoon bottom waters showed a remarkable consistency in space and in time. During the investigation the total range of temperature encountered was 28.20-28.70°C. and of salinity 34.22-34.67 $^0/_{00}$ (see station descriptions). Most of the species collected along the transect also occur in intertidal and reef flat areas (Dawson 1957) where values for the above factors greatly exceed the extremes found along the transect.

Inorganic phosphate values were consistently higher in bottom waters than in the corresponding surface waters, and there was a significant increase with depth in mean phosphate values. The highest value noted (0.509μga/l) was found at the deepest station; however this phosphate distribution was not correlated with any noted variations in algal distribution.

Algal Distribution as Related to Depth and Light

It is well established that the amount of available light decreases exponentially with depth. The lack of marked variation in other chemical and physical factors measured along the transect suggests that light is the prime factor influencing the bathymetric distribution of the lower infralittoral benthic algae of Eniwetok Lagoon. The measured light extinction values for lagoon waters (Fig. 4) show approximately a 70% reduction in available light in the upper 20 m of water, and approximately a 25% reduction in the next 40 m. This appears to be correlated with the observation that the greatest reduction in number of species with depth occurs within the 0-20 m zone.

Several other observations tend to support this view. A marked change occurs in the relative position of coral patch community populants with increasing depth in the 0-20 m zone. At the more shallow stations the algae not only grow on the lighted coral surfaces but also in well shaded crevices and holes. With an increase in depth the proportion of algae growing in shaded areas decreases, until finally on the deeper station the algae are found almost exclusively on the exposed surfaces of the coral patch.

In the lower infralittoral zone, the numbers of species did not decrease markedly with depth, but the number of individuals of any single species did. With the exception of the species which appeared to thrive at 20 to 65 m, i.e. *Dictyopteris repens, Tydemania expeditionis,* and various *Halimeda* species, the algal cover was relatively sparse.

The algae existing under reduced light conditions often did not have the morphological structure of the same species growing in the littoral and upper infralittoral zones. The most characteristic change noted was a spindly form associated with lighted pigmentation. One species in which this change was particularly noticeable was *Halimeda monile*. At the more shallow stations this species was characteristically short, with heavily calcified forms rising by a short caulescent base from a heavy holdfast with numerous "branches." With an increase in depth, the "branches" became fewer in number, smaller in relative size and more lightly calcified, while the plant in general became taller and more spindly. Pigmentation graded from dark green in the shallow water specimens to very light green in specimens from deeper water. This relationship is illustrated (Figs. 5, 6) where specimens from a graded series of depths are compared.

Other species collected seemed to show similar changes but sufficient specimens were not collected at the various depths to clearly demonstrate this gradient. For example, the ratio between the number of ramelli and the length of the stolon in *Caulerpa racemosa* seemed to decrease with depth, and to be combined with a reduction in the height and diameter of the ramelli concerned. In *Dictyota*, a marked lengthening and attenuation of the thallus was noted with increasing depth.

Distribution of the Algae as Related to Substrata

When the species-substrata relationship was examined certain facts became apparent. Some species, for example *Halimeda opuntia* and *Botryocladia skottsbergii,* were exclusively restricted to a coelenterate coral consolidated facies, and were thus partially limited by the surface area of this facies available on a particular station. Other species, growing over the surface of an unconsolidated facies, seemed to require a relatively smooth, undisturbed surface on which to develop. This was particularly true in the case of certain of the Cyanophyta which formed circular surface patches. A few species grew most profusely when the sand substratum contained numerous large particles serving as points of attachment. This was particularly evident in the case of *Dictyota* and

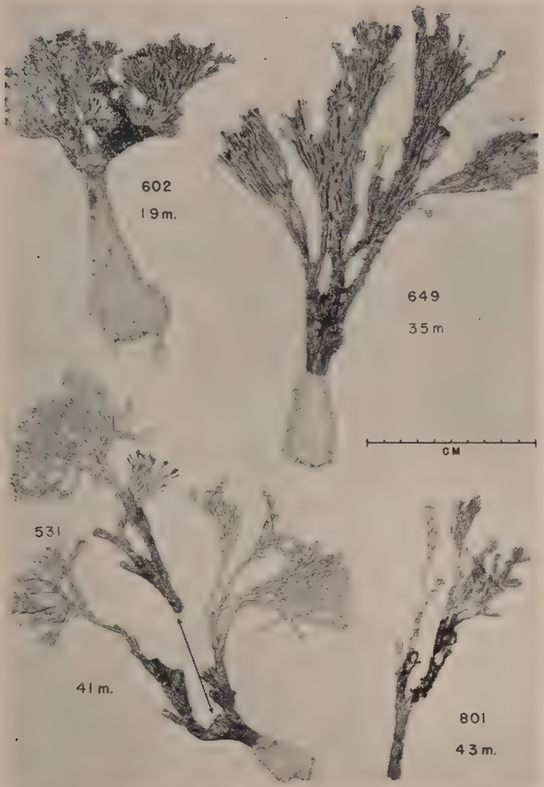


FIG. 5. Morphological changes in *Halimeda monile* collected at different depths.

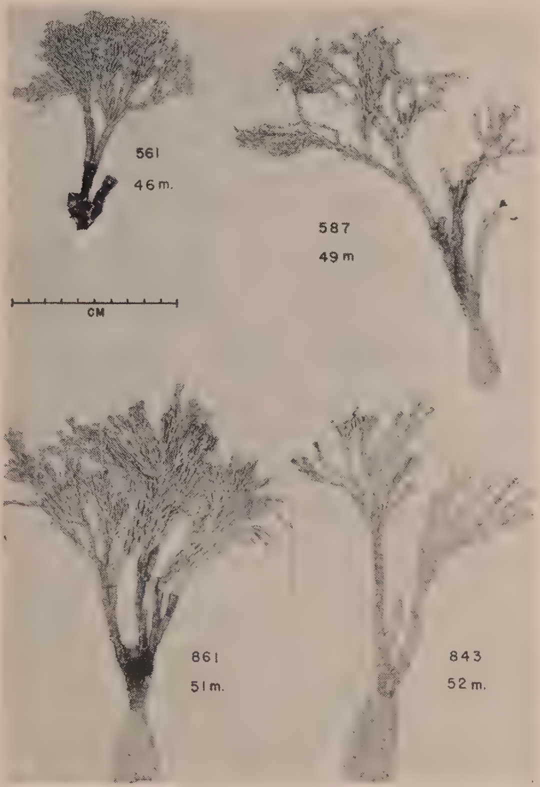


FIG. 6. Morphological changes in *Halimeda monile* collected at different depths.

Dictyoyopteris, which were similar in ecological habit. These species were occasionally collected on a coelenterate coral substratum, or found as epiphytes on *Halimeda.* They grew luxuriantly only on the sand substratum containing large particles. *Halimeda monile,* characterized by a massive holdfast, and *Caulerpa serrulata,* characterized by a spreading stolon system, were primary examples of species which grew on a sand substratum of unrestricted particle size.

Of particular note is the role that the various *Halimeda* species play as a substratum for epiphytic algae, especially among the Rhodophyta. Almost invariably the *Halimeda* species collected were epiphytized to a certain degree. In general these epiphytic species were the same ones that characterized the station colenterate coral substratum, but occasional species, such as *Sphacelaria furcigera* and *Antithamnion iherminieri* were only collected as *Halimeda* epiphytes.

Distribution of the Algae as Related to Benthic Animals

The herbivorous elements of the benthic fauna did not apear to influence the composition of the station communities. On those stations which were shallow enough for algae to grow in the depths of protected crevices, presumably out of the reach of browsing herbivores, the floral composition in the crevices appeared to be the same as that of the unprotected coral surfaces (see station descriptions). This would seem to indicate that the effects of browsing by benthic fauna were negligible. This is in contrast to situations noted by the author on Oahu reef flats, where on denuded quadrats certain algae were grazed off almost as soon as they appeared and thus were maintained as a rather minor element of the community.

The effect of the burrowing elements of the benthic fauna on the sand facies community of many of the stations was considerable. As noted on stations 2, 3, 5, and 7 on the eastern slope of the transect the sand flats between the coral patches were greatly disturbed. This disturbance evidenced itself as overlapping sand mounds 10 to 15 cm in height, composed of debris and castings from some unidentified burrowing organism. An estimated 95% of the sand facies of the affected stations were so disturbed, and gave the general appearance of being continually worked over. These bottom disturbances were restricted to a relatively narrow vertical range. The sand facies of those stations above and below this range were undisturbed.

Within this vertical range the sand facies were almost without large algae of any species. Occasional juvenile forms might be noted, but the only specimens of any size were collected on the sides and tops of apparently inactive mounds, or in those few, undisturbed areas on the station. This is interpreted to mean that the continual "churning" of the substratum by these benthic organisms has prevented algae, which might occur elsewhere on the same stations, from starting and growing to the point where they would not be "uprooted" or buried by the sand displacements. On undisturbed stations the Cyanophytan species formed patches which occasionally reached one m in diameter. On those stations with the maximum faunal activity, the patches rarely exceeded 2 cm in diameter.

SUMMARY

Utilizing self-contained underwater breathing apparatus as a research tool, an *in situ* study was made of the lower infralittoral (20-65 m) algal communities in the Eniwetok Atoll lagoon on five field trips during 1955 and 1956. Standard oceanographic determinations were made of temperature, oxygen, salinity and inorganic phosphate of the surface and bottom water of the transect stations. A surface-underwater photometer was used to obtain measurements of station *in situ* light.

During the investigation 413 collections of 95 species and varieties were made. A list of these species is presented with notes on their relative abundance and ecological habit.

The algal collections showed that 35% of the littoral and upper infralittoral reef species were capable of growth at depths from 20 to 65 m. This reduction in the number of species is primarily attributable to the reduced amount of light available at these depths.

While the available light on the deeper stations ranged from 2 to 4% of the surface light, the dominant members of the algal communities were species of Chlorophyta. The majority of stations were dominated in bulk by various *Halimeda* species, and secondarily by *Tydemania expeditionis,* and when present, in number by *Dictyopteris* or *Dictyota.* The Rhodophyta were never represented by any species which could be considered as important members of the deep water communities.

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EFFECTS OF SEED ENVIRONMENT DURING MATURATION ON SEEDLING GROWTH[1]

Plantago aristata Michx. (bracted plantain) is a successful weedy species of dry, relatively infertile sites in the Midwest. Limited studies with this species indicate that the temperature at which its seeds mature may have pronounced effects on the subsequent growth of the seedlings.

Plants were grown to maturity at a 16 hour photoperiod at constant temperatures of 60°, 70° and 80° F; seeds were harvested at each temperature when the spikes appeared brown and fully cured.[2] After storage for several months in the laboratory (at 72° F), seeds were placed in petri dishes on moistened filter paper and germinated at a 12 hour photoperiod in the 60° and 80° F constant temperature chambers; all lots germinated within 2 to 4 days. Ten to 12 days after germination, seedlings were transplanted into deep petri dishes (22 mm) containing a 10 mm layer of mineral agar (Fisk and Addoms, 1937); the transplants continued growth under the same light and temperature conditions at which the seed had germinated. Cotyledon length was measured 21 days and leaf length 65 and 120 days after germination (Table I).

TABLE I. Effect of seed maturation temperature on cotyledon and leaf length under controlled conditions

Structure and time of measurement	Temperature at which seed matured. . . °F	TEMPERATURE DURING GERMINATION AND GROWTH °F	
		60	80
Cotyledon length at 21 days[2]	60 70[3] 80	11.0 mm[1] 12.0 14.0	15.0 mm 16.0 20.0
Leaf length at 65 days	60 80	14.8 16.5	28.1 34.0
Leaf length at 120 days	60 80	23.2 30.9	21.1 30.7

[1] Average of the lengths of the longest cotyledon or living leaf from 10 plants.
[2] Days from completion of germination.
[3] 70° F seed was not carried past this time at 60° and 80° F.

Seed matured at 80° F produced larger and more vigorous seedlings than seed which had been matured at 60° F, while seed from 70° F produced seedlings of intermediate size. This relationship held whether seedlings were grown at 60° or at 80° F. Differences in leaf size and vigor persisted for 120 days under the favorable light, moisture and nutrient conditions provided in the growth chambers. Root length, although not measured, appeared to be correlated with leaf size.

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[1] This study was carried out in 1956 while the author was on the staff of Purdue University. The considerable assistance rendered by Dr. Bruce Rogers is gratefully acknowledged.

[2] Seed maturation, germination and seedling growth took place in the Controlled Climate Facilities of Purdue University. Light was supplied at an intensity of about 1000 foot candles from tungsten and fluorescent sources. Temperatures were controlled within ± 2° F.

The decrease in leaf length noted at 80° F between 65 and 120 days resulted from the death of older leaves. After 120 days plants growing at 80° F were infested with mold and some mortality had occurred; plants growing at 60° F were healthy regardless of seed source.

In a second experiment seeds were germinated directly on nutrient agar at a 12 hour photoperiod in the 70° F chamber. Results were comparable to those of the first experiment; the 80° F seed produced seedlings with larger cotyledons and leaves than the 60° F seed. In the first experiment no difference had been noted in germination rate; in the second, seed matured at 60° F germinated 1 to 2 days later than that matured at 80° F.

Seed size and weight did not appear to be responsible for the differences in growth; the relationship if any was inverse, with better growth resulting from lighter seeds. Weight per seed was determined to be 1.22 mg and 1.05 mg for 60° and 70° F seed, respectively. No 80° F seed remained, but it was presumed that it weighed less than the 60° F seed, since a sampling of seed weights of four other species of *Plantago* indicated that lower maturation temperatures (60° to 70° F) generally produced heavier seed than did higher temperatures (70° or 80° F).

Maturation of *P. aristata* seed normally occurs in Indiana during June and July; large and vigorous seedlings would be expected to result if field behavior is similar to that observed in the laboratory. Seed matured on plants during the late summer or fall would presumably produce smaller and slower growing seedlings. Possible effects of the cold winter period on seedling development are not known.

Experiments with Knox, a variety of winter wheat, have demonstrated other effects of temperature during seed maturation (Riddell and Gries 1958). Plants grown from seed matured at 60° F were found to have fewer nodes than plants grown from seed matured at 80°F. Plants from seed matured at 60° F also flowered earlier following short or intermediate exposures to cold temperature. Likewise, Stone (1957) observed that in sugar pine both storage temperature and the length of storage influenced embryo vigor. Stratification at 5° C (42° F) increased embryo vigor for stored but not for fresh seeds. Further, Went (1959) has shown that in the potato temperature conditions during vegetative growth may result in delayed effects. Cool temperatures during growth of the "seed parent" resulted in higher yields in plants of the "next generation" than were obtained when the "seed parent" was grown under warm conditions.

Koller (1955) concluded that "dormancy" as an absolute state does not actually exist and that the difference between "dormant" and "non-dormant" embryos or seeds is the degree of specificity of conditions which are necessary for germination. There appears to be ample evidence to support this view. For instance, seeds may be "dormant" at one light or temperature condition and not at another (Toole *et al.* 1955; Stearns and Olson 1958). Germination is a continuation of the process of embryological development; thus it might be presumed that seeds now designated as "non-dormant" met most of their germination requirements during prior stages in embryo development while those seeds which are "dormant" did not. It now appears that some of the conditions necessary for later vigorous growth of the seedling may also be satisfied during embryological development. In *P. aristata* seedling vigor is influenced by temperature during seed ripening, i.e. during a "dormant" period.

If it is generally true that temperature conditions prior to germination, during germination (Knapp 1956) and during vegetative growth (Went 1959) may have important consequences later in the life of the individual, then much more attention must be paid to ambient temperature at every stage of growth. The writer believes that there are many temperature responses of plants not yet well defined. Temperature effects should be anticipated in every autecological investigation, for they often relate directly to the development of plant communities.

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AUTOMATIC CONTROL OF PHOTOPERIOD

Current experiments aimed at detecting geographic variations in response to photoperiod of Douglas-fir necessitated the construction of facilities for automatic control of photoperiod.[1] Following is a description of the control methods employed.

Two growth chambers 12 ft long, 4 ft wide, and 4 ft high were constructed of wood (Fig. 1, A). Each chamber is divided into four separate compartments measuring 4 x 3 x 4 ft. The floor in each compartment is covered with a tray of sheet metal provided with a central 7 in. circular opening below which a 6 in. electric fan is mounted. This fan brings air in from below the growth chambers and up through a 7 in. stovepipe ex-

[1] These facilities were constructed as part of a project supported by a grant from National Science Foundation, NSF-G5569.

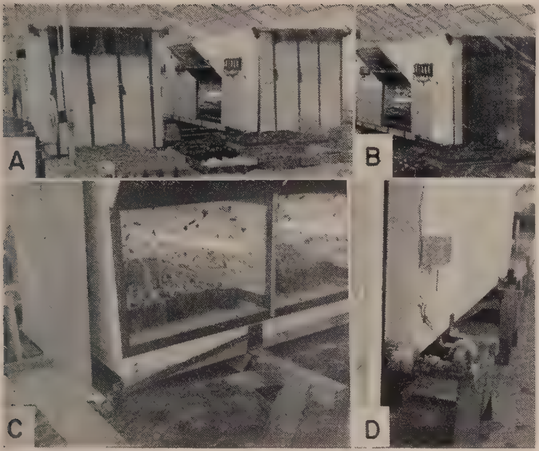

FIG. 1. General view of growth chambers when covered (A) and uncovered (B). Further explanations in text.

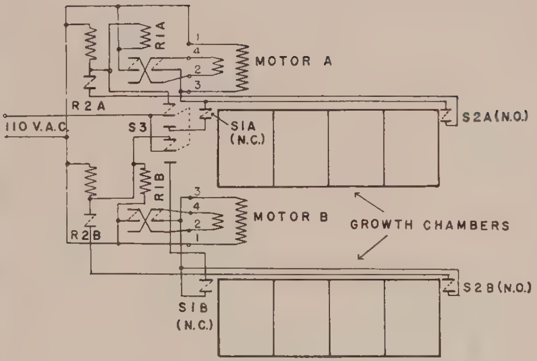

FIG. 2. Diagram of wiring system (exclusive lamps and fans). R1A, R1B-D.P.D.T. 110V A.C. relays (Guardian 200 series); R2A, R2B-S.P.S.T. 110V A.C. relays (Guardian 200 series); S1A, S2A, S1B, S2B-S.P.D.T. Microswitches. Further explanations in text.

tending one ft. into the cabinet (Fig. 1, C). In each compartment are installed six 30 Watt fluorescent tubes, 4 of them suspended 18 in. above the floor and one on each side of the cabinet. Three of the tubes are daylight tubes and the other 3 are red (arranged alternately). The ballasts of all lamps are mounted outside the cabinets to avoid heating.

Each compartment has a separate door to the outside and all walls are lined inside with aluminum foil to increase the light reflection. Both chambers rest on supports 3 ft high installed in a greenhouse.

All compartments are open above to permit daylight to reach the plants. Shortening of the natural length of day is accomplished by pulling a light-proof trucking canvas over the top of the cabinets. To one end of the canvas (13 ft v 52 in.) are attached 4 straps which go around under the chambers and are attached by means of buckles to the other end of the canvas. By this method a continuous belt of canvas (13 ft) and straps (approximately 20 ft) goes around the chambers lengthwise (Fig. 1, A). This belt travels on four 52 in. rollers of aluminum irrigation pipe mounted horizontally on pillow blocks at the upper and lower edges of each end of the chambers.

The canvas is moved by a 1/20 horsepower resistance-split-phase motor with a gear reduction to 40 RPM (Boston Gear Works). The pulley shaft of this motor is coupled directly to the axle of a 6 in. roller of aluminum (Fig. 1, D).

Since the canvas contracts and expands with changes in air humidity, one of the lower rollers (Fig. 1, C) is mounted on 48 in. long, movable steel arms attached to the lower edge of the chamber. The weight of this roller and the steel arms maintain uniform tension on the canvas and straps.

The wiring diagram[2] (Fig. 2) shows the condition for movement of the covers to the right (uncovering the cabinets). A double pole, double throw clock switch (SW3) is represented in Figure 2. When the covers no longer touch the limit switches S2A and S2B (normally open), mounted on the upper edge of each chamber, the motors stop. The relay switches Ry 1A, Ry 1B, Ry 2A, and Ry 2B remain energized until the switch S3 is reversed by the clock. When this occurs the motors are reversed and start pulling the covers to the left back up over the cabinets until they touch limit switches S1A and S1B (normally closed) which stop the motors.

The fluorescent lamps are used as supplementary light to daylight when the cabinets are uncovered. In addition they are used at various intervals during the period the cabinets are covered. The lamps in each cabinet are controlled by separate clock-switches (not shown in Fig. 2).

The light intensity in the greenhouse housing the growth chambers (glass sprayed with whitewash) is approximately 2000 foot candles at noon on clear July days. The intensity 6 in. above the floor in the chambers is about 200 foot candles at noon without the fluorescent lamps and about 400 foot candles when the lamps are used in addition to the sunlight. This is above the minimum required for normal growth by most plants and appears sufficient for the plants used in the present studies (*Pseudotsuga* and *Alnus*). The lamps alone (when the cabinets are covered) produce about 200 foot candles 6 in. above the floor.

The temperature in the greenhouse is partially controlled by an evaporation cooler. However, the temperature may fluctuate between 55-60°F during night and 85-90°F during the day. All chambers are covered simultaneously at 5 PM and uncovered at 8 AM to avoid temperature differences between chambers. Any long-day treatment is given only by light from the fluorescent lamps. To avoid temperature differences between chambers with additional light and those without light incandescent lamps painted black are installed in the latter. These lamps are controlled by the same clock switches controlling the fluorescent lamps in the chambers receiving additional light. By this means the temperature in the dark chambers is kept within plus or minus 2° F of the temperature in the lighted chambers.

These facilities permit either 4 different photoperiods replicated twice, or 8 different non-replicated photoperiods.

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SEED DISPERSAL AND MINERAL NUTRITION IN SUCCESSION IN ABANDONED FIELDS IN CENTRAL OKLAHOMA[1]

Introduction

In a study in the southern Great Plains, Savage and Runyon (1937) found that none of the abandoned fields possessed a cover comparable in composition with the climax of the region, even after 40 years. Tomanek *et al.* (1955) reported that the climax composition had not been attained in a field in central Kansas which had been abandoned for 33 years. Booth (1941) found that succession in abandoned fields in central Oklahoma included four stages: (1) weed, (2) annual grass, (3) perennial bunch grass, and (4) true prairie. The weed stage lasted only 2 to 3 years. The annual grass stage lasted from 9 to 13 years and was dominated by triple awn grass, *Aristida oligantha*.[2] The perennial bunch grass stage was dominated by little bluestem, *Andropogon scoparius*, and this stage was still present 30 years after abandonment. This was the oldest abandoned field studied by Booth so he was not able to ascertain how long a period is required for the return of the true prairie, which in central Oklahoma is dominated by little bluestem, big bluestem (*A. gerardi*), switch grass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*).

The very slow invasion of abandoned fields by climax grasses, even when such species completely surround the fields, has always been quite puzzling. One possible explanation, of course, is that fruits of the climax species containing viable seeds are not dispersed very far from the parent plants. One phase of this project was concerned with a study of the distance of dispersal of such fruits of little bluestem. After dispersal, the fertility of the soil may determine which species become established. In a preliminary experiment using soil (top 3 in.) from a field abandoned for 12 years it was found that triple awn grass, which comes in fairly early in abandoned fields, was able to grow rapidly and produce seeds. Little bluestem, which comes into such fields in the next stage of succession, was unable to grow in the same soil without the addition of fertilizer. Another goal of the present project, therefore, was to determine the relative nitrogen, phosphorus, and potassium requirements of triple awn grass, little bluestem, and switch grass which enter during different stages of succession in old fields.

Methods and Materials

Dispersal Tests

In November, 1953, soil samples consisting of cylinders 6 in. in diameter and 3 in. deep were taken at various distances from an isolated cluster of little bluestem plants in a revegetating old field (abandoned 12 years) in the University of Oklahoma Grassland Plots located 8 miles west of Norman, Oklahoma. The cluster of plants occupied an area about 12 ft in diameter. Four soil samples were taken from within the cluster of plants and two samples were taken at each of the following locations: 6 ft, 12 ft, 24 ft, and 48 ft north of the edge of the cluster. A similar series were taken south of the aggregation (Table I). Each soil sample was spread in a fairly thin layer over a sand base in a 12 in. pot in the greenhouse. The sand was previously heated to a temperature of 150° C for 4 days to insure that no viable seeds were present in it. The soil was watered as necessary with rainwater. The pots were checked regularly for the presence of little bluestem seedlings, and all other types of seedlings were removed whenever they appeared to eliminate any possible competition.

Table I. Distance of dispersal of seeds of little bluestem from an established clump in a revegetating old field. Prevailing wind during most of year from south

Dist. and Dir. from Edge of Est. Clump	No. of Soil Samples Taken	No. of Samples with Seedlings of Little Bluestem
0	4	4
6 ft. north	2	2
12 ft. north	2	0
24 ft. north	2	0
48 ft. north	2	0
6 ft. south	2	1
12 ft. south	2	0
24 ft. south	2	0
48 ft. south	2	0

Tests of Mineral Requirements

Fruits of little bluestem, triple awn grass, and switch grass were collected from Oklahoma sources and planted in flint shot quartz sand in 4 in. glazed pots in the greenhouse. Hoagland's No. 1 culture solution was the basic one used for all tests. In Experiment 1, plants of each species were grown in complete solution, and in solutions containing either 1/10, 1/100, or 1/1000 as much nitrogen (N) or phosphorus (P) as occurred in the complete solution. Plants of each species were also grown in a solution containing 1/23 of the potassium (K) in the complete solution, thus making a total of 8 different solutions. All major elements were kept constant except the one being tested, and the pH of each solution was adjusted to 5.5. The amounts of N, P, and K in the control solution are given in Table II. In all cases the plants were thinned to 5 per pot. Eighteen pots of each species were watered with the complete solution and 6 pots of each were watered with each of the other 7 solutions, making a total of 60 pots for each species. All plants were kept on a 17-hour day-length by extending the light period with incandescent bulbs; all plants were watered at the same time with equal amounts of the appropriate solution. The plants were allowed to grow for 3 months, at which time they were harvested and the oven-dry weights of roots and shoots determined.

The same procedures were followed in Experiment 2 as in Experiment 1 with the following exceptions. The solutions used were: complete, N/20,/ N/40, N/80, P/20, P/40, P/80, K/20, K/40, and K/80. The pH of each solution was adjusted to 5.85. At the time of harvesting the number of tillers on each plant was determined.

Results and Discussion

Dispersal Studies

Little bluestem seedlings appeared in all soil samples taken within the cluster of plants of that species in the field, in both soil samples taken 6 ft north of the periphery of the cluster, and in one soil sample taken 6 ft south of the cluster (Table I). No seedlings of this species appeared in any of the other samples. It appears, therefore, that even with the high wind velocities which

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[1] Supported in part by a grant from the University of Oklahoma Alumni Foundation.

[2] Nomenclature follows Hitchcock and Chase (1950).

Table II. Experiment 1—Comparison of nitrogen, phosphorus, and potassium requirements of three species of grasses important in different stages of old-field succession in central Oklahoma

Min. Concn.	Plant Part	Aristida oligantha % of Control Wt.	Aristida oligantha Shoot-Root Ratio	Andropogon scoparius % of Control Wt.	Andropogon scoparius Shoot-Root Ratio	Panicum virgatum % of Control Wt.	Panicum virgatum Shoot-Root Ratio
Control*	Shoots	100	2.26	100	1.97	100	1.65
	Roots	100		100		100	
N/10	Shoots	48.6	1.85	44.3	1.20	46.9	1.11
21 ppm	Roots	59.5		72.5		69.8	
N/100	Shoots	9.5	1.17	4.9	0.82	7.4	0.49
2.1 ppm	Roots	17.8		11.8		25.1	
N/1000	Shoots	6.0	1.36	1.3	0.68	3.0	0.69
0.21 ppm	Roots	9.2		3.9		7.1	
P/10	Shoots	79.9	2.16	62.0	2.01	53.8	1.18
3.1 ppm	Roots	83.4		60.7		75.2	
P/100	Shoots	5.0	1.14	1.0	1.14	1.7	0.82
0.31 ppm	Roots	9.8		1.9		3.5	
P/1000	Shoots	4.6	1.20	1.3	1.18	1.5	0.29
0.031 ppm	Roots	8.6		2.2		8.8	
K/23.0	Shoots	75.5	1.95	59.4	2.20	64.9	1.66
10.63 ppm	Roots	87.1		53.2		64.4	

* Control solution (Hoagland's No. 1) contained among other things the following amounts of N, P, and K: 210 p.p.m. of N, 30.98 p.p.m. of P, 244.9 p.p.m of K.

are common in Oklahoma, fruits of little bluestem containing viable seeds are not commonly carried much over 6 ft from the parent plants. It is possible that animals may transport the fruits much farther. Nevertheless, it seems quite probable that the rather slow invasion of abandoned fields by little bluestem and other climax species may be at least partly due to the short distance of dispersal of viable seeds of those species by the wind. We have followed the invasion by little bluestem of a 3-acre abandoned field near Norman for several years, and have noted that with the exception of a few isolated plants, the invasion has occurred slowly around the periphery of the field. The fruits and even the entire plants of triple awn grass are often carried fairly long distances by the wind. This is probably partially responsible for the earlier invasion of abandoned fields by triple awn grass.

Mineral Requirements

In the low-nitrogen solutions, the shoot growth of triple awn grass was consistently somewhat better in comparison with its control than was that of little bluestem or switch grass (Table II). The shoot growth of switch grass was slightly better than was that of little bluestem in the same low-nitrogen solutions. Root growth did not follow such consistent trends. The overall result was that the shoot-root ratio tended to remain fairly high in triple awn grass while it dropped to a fairly low value in each of the other two species.

The growth of both shoots and roots of triple awn grass was better than for the other species in the low-phosphorus solutions with the exception of the roots of switch grass in the P/1000 solution (Table II). The shoot-root ratios of triple awn and little bluestem were comparable in the various phosphorus solutions, but that of switch grass dropped to a very low value in the lowest phosphorus solution.

All species grew quite well on the K/23 solution, with both the shoot and root growth of triple awn grass being slightly better than that of either of the other species (Table II). The shoot and root growth of switch grass was slightly better than in little bluestem. The shoot-root ratios of all species remained about the same as in the control plants.

In the experiment discussed above, all species grew fairly well on the solutions containing one-tenth of the phosphorus or one-tenth of the nitrogen in the complete solution. All species had a relatively limited growth on the solutions containing one-hundredth or one-thousandth of the nitrogen or the phosporus in the control. It was decided, therefore, to perform a similar experiment using amounts of N, P, and K between one-tenth and one-hundredth of the amounts in the complete solution.

In the second experiment, the shoot growth of triple awn was again consistently better than that of little bluestem or switch grass on the low-nitrogen solutions (Table III). The shoot growth of little bluestem was slightly better than that of switch grass on all the low-nitrogen solutions. Root growth did not follow such consistent trends, although the root growth of little bluestem on the low-nitrogen solutions was consistently better than that of switch grass. As in Experiment 1, the shoot-root ratio remained fairly high in triple awn, whereas it dropped to a relatively low value in little bluestem and switch grass (Table III).

The growth of both shoots and roots of triple awn was better than in the other species in all low-phosphorus solutions in Experiment 2 with the exception of root growth in little bluestem in the P/20 solution (Table III). The growth of both shoots and roots was slightly better in little bluestem than in switch grass except in the P/40 solution. The shoot-root ratios of little bluestem and switch grass declined more on all low-phosphorus solutions than did that of triple awn, with the exception of switch grass in the P/80 solution.

All species grew at least moderately well on all low-potassium solutions (Table III). There were no consistent trends in shoot growth, all species growing about equally well on all solutions. Little bluestem had consistently better root growth on the low-potassium solutions than did either of the other species. Moreover, the root growth of switch grass was consistently slightly better than that of triple awn. The shoot growth of triple awn in the K/20 solution was almost identical with that of the same species in the K/23 solution in Experiment 1; but for some reason which is not clear, the root growth was considerably less in Experiment 2. The shoot-root ratios of all three species in the low-potassium solutions were about the same as they were in the respective controls or higher.

The amount of tillering, as compared with the respective control plants, was consistently higher in triple awn on the low-nitrogen and low-phosphorus solutions

Table III. Experiment 2—Comparison of nitrogen, phosphorus, and potassium requirements of three species of grasses important in different stages of old-field succession in central Oklahoma

		Aristida oligantha		Andropogon scoparius		Panicum virgatum	
Min. Concen.	Plant Part	% of Control Wt.	Shoot-Root Ratio	% of Control Wt.	Shoot-Root Ratio	% of Control Wt.	Shoot-Root Ratio
Control*..........	Shoots	100	2.55	100	3.06	100	2.32
	Roots	100		100		100	
N/20..............	Shoots	38.0	1.33	27.0	1.46	15.7	1.24
10.5 ppm..........	Roots	72.6		56.3		29.4	
N/40..............	Shoots	18.9	1.45	10.4	0.94	7.8	1.13
5.25 ppm..........	Roots	33.3		33.5		16.0	
N/80..............	Shoots	16.6	1.90	7.5	0.82	5.9	1.03
2.62 ppm..........	Roots	22.2		28.0		13.4	
P/20..............	Shoots	22.9	2.44	15.3	1.65	11.2	1.26
1.55 ppm..........	Roots	23.8		28.3		20.5	
P/40..............	Shoots	13.9	1.58	7.5	1.50	8.3	1.19
0.78 ppm..........	Roots	22.5		15.4		16.2	
P/80..............	Shoots	3.2	1.43	1.3	1.18	1.0	1.27
0.39 ppm..........	Roots	5.7		3.4		1.8	
K/20..............	Shoots	74.5	6.14	81.1	2.59	62.3	2.47
11.72 ppm.........	Roots	30.9		95.7		58.4	
K/40..............	Shoots	43.3	6.36	44.4	2.81	47.7	3.80
5.86 ppm..........	Roots	17.3		48.3		29.1	
K/80..............	Shoots	40.6	5.16	36.9	3.11	35.2	3.83
2.93 ppm..........	Roots	20.0		36.3		21.2	

* Control solution (Hoagland's No. 1) contained among other things the following amounts of N, P, and K: 210 p.p.m. of N, 30.98 p.p.m. of P, 234.5 p.p.m. of K.

Table IV. Experiment 2—Effects of different levels of nitrogen, phosphorus, and potassium on tillering (at age 3 mo.) in three species of grasses important in different stages of old-field succession in central Oklahoma

	ARISTIDA OLIGANTHA		ANDROPOGON SCOPARIUS		PANICUM VIRGATUM	
Mineral Concentration	Avg. no. of tillers	% of Control	Avg. no. of tillers	% of Control	Avg. no. of tillers	% of Control
Control*......	6.9	100	5.2	100	3.8	100
N/20 10.5 ppm	2.0	29.5	1.1	21.6	0.8	21.8
N/40 5.25 ppm	0.9	12.7	0.4	7.3	0.03	0.8
N/80 2.62 ppm	0.3	4.4	0.2	3.8	0.1	1.8
P/20 1.55 ppm	1.0	14.0	0.8	14.8	0.3	7.1
P/40 0.78 ppm	0.5	6.7	0.1	1.9	0.2	4.5
P/80 0.39 ppm	0.04	0.6	0.00	0.0	0.00	0.0
K/20 11.72 ppm....	4.5	65.5	3.9	75.3	2.2	57.7
K/40 5.86 ppm....	3.1	45.6	2.2	42.1	2.3	59.6
K/80 2.93 ppm....	2.8	40.5	2.6	50.4	2.1	55.1

* Control solution (Hoagland's No. 1) contained among other things the following amounts of N, P, and K: 210 p.p.m. of N, 30.98 p.p.m. of P, 234.5 p.p.m. of K.

than in the other species with one exception (Table IV). In the P/20 solution the relative amounts of tillering were about the same in triple awn and little bluestem. The relative amount of tillering was generally higher in little bluestem than in switch grass in the low-nitrogen and low-phosphorus solutions. There were no consistent trends in relative numbers of tillers in the three species in the low-potassium solutions. Actually, all species tillered quite well in all low-potassium solutions.

The results discussed above indicate that triple awn has a somewhat lower requirement for nitrogen and phosphorus than do little bluestem and switch grass. The fact that triple awn is able to maintain a fairly high shoot-root ratio even on very low amounts of phosphorus and nitrogen is probably extremely important in enabling it to reproduce and survive in soil which is very low in these elements. Little bluestem appears to have a slightly lower requirement for nitrogen and phosphorus than does switch grass. The differences in the requirements of these two species are certainly not as clear-cut as the differences between triple awn and the other two species.

Consistent differences in the three species in their requirements for potassium are not apparent. It is certainly clear that all three have a very low potassium requirement.

As pointed out previously, the order of invasion of abandoned fields in Oklahoma by the three species under investigation is as follows: (1) triple awn, (2) little bluestem, and (3) switch grass. This is apparently the order of increasing nitrogen and phosphorus requirement also. The question still arises, however, as to whether this is just a coincidence or whether a causal relationship exists. Is there any definite evidence that abandoned fields are low in nitrogen and phosphorus, and what is the status of potassium in such soils?

As indicated in the introduction, soil from the abandoned field in the University of Oklahoma Grassland Plots would not support the growth of little bluestem without added fertilizer, while triple awn grass grew and reproduced without any additions. Daniel and Langham (1936) found an average decrease of 15% in total nitrogen due to cultivation in the top 12 in. of soil in the Oklahoma panhandle as compared with virgin soils. Finnell (1933) reported an average decline in total nitrogen in the top 6 ft of soil at the Oklahoma Panhandle Agricultural Experiment Station farm of 50 lbs per acre per year during the first 22 years the land was cultivated. Chaffin (no date) stated that in less than half a century of cultivation in Oklahoma, ". . . the soils have lost 30 to 35% of their nitrogen. . . ." Swanson (1915) found in Kansas soils that from 22.6 to 43.5% of the nitrogen, based on the virgin soil content, was lost through cultivation. Puhr and Olson (1937) reported a loss of nitrogen of from 7 to 59% as compared with the virgin condition in South Dakota soils cropped from 50 to 55 years.

Losses of phosphorus due to cultivation have been similarly demonstrated. Puhr and Olson (1937) found appreciable losses of phosphorus in South Dakota soils due to cropping. De Turk *et al.* (1927) estimated a loss of 6 lbs of phosphorus per acre per year due to cultivation of Illinois soils. Harper (1932) reported that more than 50% of the soils tested from the eastern half of Oklahoma were found to be deficient in easily soluble phosphorus. Subsurface soils were found to be lower in this element than surface soils; many subsurface soils in eastern Oklahoma were found to be extremely low in easily soluble phosphorus. Removal of the surface soil by erosion leaves a very infertile soil. Most fields abandoned from cultivation have generally been seriously eroded prior to abandonment.

As indicated above, cultivation seems to bring about a decrease in the nitrogen and phosphorus content of the soil. When one considers the fact that generally only the most infertile, badly eroded fields are abandoned, it seems quite likely that the nitrogen and phosphorus contents of such fields are usually quite low at the time of abandonment.

In regard to potassium, Harper (1950) reported that cropping for a period of 30 to 50 years had not seriously reduced the total or exchangeable potassium content of Oklahoma soils. Virtually the only soils which were found to be low in potasisum were those which were low in this element in their virgin condition. Actually only 18% of the large number of soil samples tested from all of Oklahoma were found to be low in exchangeable potassium and most of the very low samples came from the eastern portion. It appears from Harper's work that potassium is not as likely to be deficient in abandoned fields as are nitrogen and phosphorus.

Although no definite causal relationships have been established, the evidence presented above makes it appear quite possible that the low nitrogen and phosphorus requirement of triple awn grass may be important in enabling it to become established in abandoned fields considerably earlier than little bluestem or switch grass. Moreover, the fact that little bluestem has a slightly lower nitrogen and phosphorus requirement than switch grass may help to account for the earlier ecesis of little bluestem in such old fields. If the fertility of the soil is of significance in determining the order of ecesis of the three species under consideration, as appears likely, potassium probably does not play a very important role. There were no clear-cut differences in the requirements of the three species for potassium, and the evidence from other studies suggests that the potassium content of abandoned field soils in Oklahoma is probably not usually very low.

Harper *et al.* (1934) analyzed a large number of plants for their nitrogen and phosphorus content, and found triple awn grass to be exceedingly low in these elements during all its stages of growth. Little bluestem and Indian grass, which come in at successively later stages, had higher amounts of nitrogen and phosphorus. Indian grass had the highest average content of each of the elements. Daniel (1932) found the amounts of phosphorus and nitrogen in switch grass to be higher than in little bluestem and Indian grass. It is a well known fact that the amount of an element actually absorbed by a plant does not necessarily indicate the exact need of the plant for that element. It is perhaps worth noting however, that the relative average amounts of nitrogen and phosphorus in triple awn grass, little bluestem, and switch grass correlated nicely as reported above with the relative requirements of these species for those elements as demonstrated in the present experiments.

Harper *et al.* (1934) found that almost all the annual and perennial "weeds" (forbs) which come in during the early stages of succession in abandoned fields had much higher contents of nitrogen and phosphorus than did any of the grasses analyzed. Apparently, many of the forbs root fairly deeply and thus bring minerals from the deeper layers of the soil to the surface. The growth of such species on abandoned land ". . . probably produces a marked influence on the availability of mineral matter in the soil," as suggested by Harper *et al.* (1934). It certainly appears possible that forbs which invade abandoned fields influence succession by increasing the availability of nitrogen and phosphorus in the surface layers of the soil, thus enabling plants with successively higher requirements for these elements to become established gradually in the order of their increasing needs for nitrogen and phosphorus.

SUMMARY

1. In an effort to explain why triple awn grass, little bluestem, and switch grass come in at different stages of succession in revegetating old fields in central Oklahoma, a brief study of fruit dispersal in two of the species was made, and a more thorough investigation of the nitrogen, phosphorus, and potassium requirements of all three species was carried out.

2. Fruits and even entire plants of triple awn, which is the first of the three species to invade abandoned fields, have been observed to be carried fairly long distances by the wind. Fruits of little bluestem containing viable seeds were found to be dispersed by the wind apparently only slightly over 6 ft from the parent plant. This probably helps to account for the slow invasion of rather small abandoned fields by little bluestem, such invasion starting around the margin and moving slowly inward year by year.

3. The apparent order of the three species based on increasing requirements for nitrogen and phosphorus was found to be as follows: (1) triple awn grass, (2) little bluestem, (3) switch grass. This is the relative order in which the three species invade abandoned fields.

4. There were no consistent differences in relative requirements of the three species for potassium. Actually all species grew quite well in all low-potassium solutions.

5. Studies of other workers have indicated that soils of abandoned fields in Oklahoma are probably usually low in phosphorus and nitrogen at the time of abandonment, but are probably not usually deficient in potassium.

6. It certainly seems possible, on the basis of the evidence obtained, that the relative requirements for nitrogen and phosphorus of triple awn grass, little bluestem, and switch grass may be of considerable importance in determining the order of establishment of the species in abandoned fields.

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TWO APPLICATIONS OF A METHOD OF DETERMINING THE ERROR OF POPULATION ESTIMATES OF MOSQUITO LARVAE BY THE MARK AND RECAPTURE TECHNIQUE[1]

The mark and recapture technique has frequently been used to estimate field populations of various animals and there are several analyses to determine its error. Such analyses usually incorporate a factor for natural mortality and base the error on a single recovery sample. In the following experiments natural mortality could be disregarded because of the short duration of the experiments, and several samples could be taken simultaneously throughout the small pool. A method for determining the error under these conditions was devised with the help of the Statistical Laboratory, Canada Department of Agriculture, Ottawa, and is described below as well as its application to two problems concerning numbers of mosquito larvae.

The tagging with radioactive phosphorous, release, and recovery were described by Baldwin *et al.* (1955). Twenty-four hours after the release of radioactive larvae 3 or 5 samples of about 150 larvae each were collected and the ratio of the numbers of tagged larvae to the total number of larvae determined. These ratios were substituted in the following equations to estimate the population and to determine the error of the estimate for each date (Table I).

Let X = number of tagged larvae in population and Y = number of untagged larvae in population; then $Z = X + Y$ = total population. Let x = number of tagged larvae in sample, and y = number of untagged larvae in sample; then p, the recovery ratio, =

$$\frac{x}{x+y} =$$

the fraction of tagged larvae in the sample.

The population estimate obtained from a series of samples containing a total of n larvae is then

$$\hat{Z} = X/p_T$$

where X is known, without error, and the p_T ratio is based on the total larvae in all of the samples. Since

$$(dZ)^2 = \left(\frac{X}{p_T{}^2}\right)^2 (dp_T)^2,$$

the variance of $\hat{Z}$ is given approximately by

$$S\hat{Z}^2 = \left(\frac{X}{p_T{}^2}\right)^2 S_{p_T}{}^2.$$

$S_{p_T}{}^2$ will equal $p_T \dfrac{(1-p_T)}{n}$ when the tagged larvae are randomly distributed in all samples. The validity of this assumption of randomness may be tested by the χ^2 test of the observed variance against the binomial variance in the method described by Goulden (1952). Tests of the data in the following experiments showed that the tagged larvae were randomly distributed in all samples except possibly those of May 5 and May 11 where the χ^2 value fell between the 5 and 10% level. In calculation of the error of the estimate on these 2 dates the binomial standard error was multiplied by the heterogeneity factor, $\sqrt{\chi^2/\text{d.f.}}$ This factor was $\sqrt{5.204/2} = 1.6$ for May 5 sample and 1.7 for the May 11 sample.

When the tagged larvae are clearly not randomly distributed the binomial error is not applicable and the error must be determined empirically from replicate samples.

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[1] Contribution No. 3711, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

TABLE I. Release and recovery of tagged mosquito larvae, and estimates of the populations and densities of larvae in 2 pools at Chatterton, Ontario, in the spring of 1954

Date of release	Number released	Total No. of mosquitoes caught, $x + y$	Recovery ratio p_T	Standard error of p_T	Estimated population	Pool area (sq. m.)	Estimated density (thousands per sq. m.)
PERMANENT POOL*							
April 14	4,300	505	.2396	.0190	17,900 ± 1,423**	12.3	1.5±0.12
April 22	9,100	316	.7025	.0257	13,000 ± 473	7.7	1.7±0.06
May 5	3,800	761	.5480	.0288***	6,900 ± 360	6.2	1.1±0.06
May 11	3,500	332	.6536	.0444***	5,400 ± 360	5.7	0.9±0.06
TEMPORARY POOL*							
April 9	1,855	1,388	.01535	.00335	117,000 ± 24,740	15.2	7.7±1.6
April 17	1,372	613	.02447	.00624	56,100 ± 14,300	11	5.1±1.3
April 30	2,040	588	.06463	.0101	31,600 ± 4,900	10	3.2±0.5

* Permanent pool, 3 samples; temporary pool, 5.
** Standard error.
*** Include correction by heterogeneity factor.

Baldwin *et al.* (*loc. cit.*) used radioactive phosphorous to tag larvae for population estimations and to identify predators in 4 walled-off bays of a permanent pool. They found an apparent decrease in numbers of larvae associated with an increase in predator numbers and with an increase in the percentage of predators that were radioactive from consuming radioactive prey. Though the estimates of prey numbers suggest a decrease, the statistical significance of it could not be determined without estimating the error associated with the estimate for each date. The errors derived from the above equations are shown with the estimates on Table I. There is obviously little overlap in the estimates so that the decrease in prey numbers was real. The p values differ slightly from those of Baldwin *et al.* (1955) in which small numbers of larvae taken for species and age determination were accidently excluded, but are included in the present calculations.

In a second application the technique was used to estimate the density of mosquito larvae in a temporary pool for comparison with that of the permanent pool. Estimations were made on 3 dates to determine if the population density changed. Table I shows that the density is of a higher order in the temporary than in the permanent, but that a similar decrease in density occurred in both types of pools with the advance in the season. The higher density of the temporary pool probably results from the concentration of larvae from a larger area than that surrounding a permanent pool. Since the magnitude of the decrease in density is similar in both types of pools, then predation may be of equal importance in the temporary pool.

The errors of the temporary pool are proportionately larger than those of the permanent pool, even though 5 samples were taken in the former and 3 in the latter. This probably results from the greater variation in depths and length of the shoreline and the consequent irregularity in the distribution of introduced larvae in temporary as compared to permanent pools. More sampling might have overcome the problem of distribution.

Another factor is apparent in a comparison of the recovery ratios and the errors of the estimates. In the temporary pool where the errors are large, the ratio of tagged to total larvae exceeded .05 only once whereas in the permanent pool the ratio averaged as much as 10 times this value. The estimate of April 14 in the permanent pool also illustrates this feature; a large error is associated with a low recovery ratio. The size of the error obviously depends on the percentage of tagged larvae in a sample, and thus on the percentage of tagged larvae in the population.

This technique and analysis are easy to use in the field but the following limitations need consideration: a large number of larvae should be tagged; the experiment must be of short duration; as many samples as possible should be taken; and the technique in general is more satisfactory in permanent or discrete pools.

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A CLASS EXERCISE ON A MARINE MICROCOSM

This is a report on a class exercise which was a response to a challenge: to go beyond the ecological survey to a total, quantitative analysis of an ecosystem but without losing sight of individual species. The numbers of species and the ecological complexities of most communities panic students; on the other hand, when the organisms are categorized in an over-simplified scheme and gross extrapolations made from small samples, he is certainly left with the impression of implausible generalizations. The solution is restriction of study to a habitat of very small size and a community of few species, in this instance a high intertital rock pool. Other equally suitable situations will occur to the reader.

The opportunity for this study came during the summer of 1958 while teaching the Marine Ecology course at the Hopkins Marine Station of Stanford University at

Pacific Grove, California. The two term course started with systematic surveys of many habitats, considering conditions of existence and resulting in species lists. The second term was concerned with population and community ecology including textual reading, lecture, student reports on current literature, individual projects, and the group effort on our rock pool microcosm.

To foster research attitudes, we were determined to be as non-directive as possible. A small, semi-isolated, and seemingly barren permanent rock pool was found and the question posed: What could be learned about this pool in five weeks? The modest primary objectives of the class were: (1) describe the environment, (2) measure the environmental factors on a daily basis, (3) determine the species present. The site became "our little pool" and shortly OLP, which epithet became a symbol of the intensity of the cooperative effort.

THE ENVIRONMENT AND BIOTA

The pool was high between two of the jutting, rocky headlands of the highly eroded, coarsely granitic shoreline. It was mapped and photographed; elevation was determined from a nearby bench mark. The basin of the pool was somewhat greater than a square meter, had a minimum of 174 liters of water, and a rock surface area of 2.5 square meters. Three sides were steep and about one-half meter in height; the fourth side opened through a channel to the sea and to a larger pool shoreward (Figure 1).

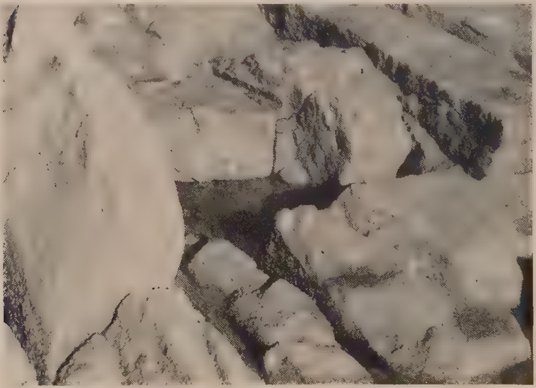

FIG. 1. The study site. Note the isolated position and the barren impression.

Recordings were made 3 times daily of pool and sea temperatures, and of the weather, sea and tide conditions. Determinations of salinity and oxygen were also made.

Analyses of these physical data pointed immediately to the important role of the sea's proximity. The water was replenished daily with high tide; since the pool was but one meter above mean high tide, even a slight swell caused a surge of white water. At time of high seas the wave shock became enormous. Between tides, the water level in the pool dropped to a depth of 30 cm in the deepest parts. During periods of replenishment, pool temperatures corresponded to those of the sea (at the time of study, 14-18 degrees C). However, between tidal surges water temperature followed the air temperature with afternoon readings of up to 25°C and evening recordings of lower than sea temperatures.

The chemistry of the pool's water also closely reflected that of the sea. For instance, the salinity was consistently the same as that of sea water. Oxygen readings during the surge of saturated sea waters were naturally identical with the sea, but during quiet water metabolically induced changes occurred. During darkness, straight line drops from saturation to lows of 33% were recorded; in hours of day light increases to as high as 112% saturation were noted.

With respect to the habitat the class was impressed with four concepts: (1) Our habitat was not really isolated; it was very dependent on sea and air conditions. (2) Of the environmental variables, only a few such a wave shock, temperature, and oxygen content reached extremes. (3) The living things and their environment were involved in nicely demonstrated action and reaction, *i.e.*, the exclusion of certain species might have been due to periodic low oxygen levels, yet these low levels were themselves a result of community metabolism. (4) Most importantly, the need for at least an annual study was painfully apparent.

The first real triumph of the microcosm approach was the compilation of a species list. Included were 2 species of fishes, 5 echinoderms, 19 mollusks, 9 crustaceans, 8 annelids, 1 sipunculid, 1 flatworm, 1 nematode, 2 protozoans, 5 algae, and 9 bacteria, these latter not identified but known from nearby pools. Of this list, 45 species were macroscopic animals and 2 were prominent species of algae. While some microscopic forms were no doubt missed, the class had a confidence in the accuracy of the species list not possible in a larger habitat where errors of sampling are prominent.

COMMUNITY STRUCTURE

The descriptive objective accomplished, we next investigated population sizes and vertical and horizontal patterns of distribution. This was possible only by virtue of the limited system. Every macroscopic animal was removed, counted, and returned, except the barnacles and tube worms which were counted in place. New species were found in the crevices and debris and a surprising total of 5,185 individuals was computed, including 23 sipunculids, 1670 barnacles, 36 sea urchins, and 1 chiton.

When each species was mapped, it was clear that OLP contained largely cryptic forms; the crevices were the centers of distribution. Only the wave tolerant limpets appeared to be randomly spread. The 2 major algae, a coralline, and a *Protococcus*-like green, had distinct patterns; the former occupied the shaded walls and crevices while the latter formed a green stain over brightly illuminated areas.

Vertical stratification was striking even in such a small habitat. The 2 littorine snails were above and below the quiet water line. The barnacles had a sharp lower limit at that line; such species were in fact only high water residents of the pool.

While our complete census and distribution maps were accurate, day to day observations indicated more fluidity in populaion size and place than these static data indicate. After several releasings of hundreds of marked snails (*Tequla funebralis*), it was found that as many as 50% left and entered the pool in a day. Continuous census of this population showed a fluctuation about a mean. Several of our species populations were in this way loci of transient individuals.

During a 25 hour natural history watch, a record was kept of all activities including the tracks of many marked individuals and another classical ecological doctrine was "discovered": the activity and composition of nocturnal and diurnal communities may be vastly different. Several species not on our day list entered at night, active feeding was prominent and many of the crevice aggregations were seen to disperse at night. Even sea urchins moved from one side of the pool to the other. The snail *Acanthina spirata* was seen to move to the barnacle belt where they apparently fed. Only the limpets, of the motile forms, did not move much day or night, contrary to the several reports of nocturnal wandering and homing.

It was clear that no species was unique to our pool, but our little community was different from any in the area and could be considered as a unit. Particularly from the natural history studies, the next phase of the study was dictated.

Community Dynamics

A systematic study of food habits was done by field observation, laboratory feeding, and by laborious stomach analyses. We constructed a generalized food web and had a remarkable demonstration of exactly what would have been expected; the pool contained producers, consumers and reducers. The really significant conclusion forced upon the class was the extreme complexity of a food web if individual species were considered. Filter feeders and strict grazers could be distinguished, but not higher trophic levels. All of our carnivores revealed themselves as euryphagous. The crabs ate other crabs, fish, snails and egg masses but also algae and washed-in eel grass. The cottid fish was equally euryphagous. The basically herbivorous sea urchins were seen to eat a chiton. We debated without conclusion whether this feeding latitude had general ecological implications or was a function of the very limited food resources of high tide pools.

While we had a food chain based on resident algae, the exogenous nutrients could not be ignored. The plankton count of the pool was less than one per liter although it was high in the adjacent sea, particularly during nocturnal vertical migrations. This disparity must be a function of wave shock or efficient filter feeders. A measure of detritus was obtained by filtering a large portion of the pool's volume; the sample was dried overnight at 60° C and reduced to ash in a muffle furnace at 600° C. For the entire pool during quiet water, we obtained the low dry weight value of .80 grams and .30 grams organic content. However, when vigorously stirred, detritus from the crevices increased the reading to 5.11 grams dry weight and 3.55 grams organic content.

Determination of the standing crops followed; the necessity for weighing each population at the time the pool was gutted for census now became clear. We had the total wet weights of the 7 species which comprised 97% of the animal bio-mass. The dry weights and organic content were determined from sample individuals. The total wet weight (shells included) of these populations was 2,284 grams compared to the value for their organic content of 170 grams.

The growth form of the encrusting coralline, *Lithophyllum* sp, and the unidentified green alga, made census and weighing impossible. Sampling was unavoidable. Measured areas of the coralline were scraped off and weighed; and with a known pool area of the species, total wet and dry weights were extrapolated. These were 845 grams and 591 grams respectively; 47 grams were lost on ignition. The green alga was impossible to remove but a comparative value was obtained by methanol extraction of chlorophyll from a rock fragment with a measured green surface. This very sharp color value was compared with an extraction of a known weight of *Ulva* sp., also a fragile green alga. On the basis of this *"Ulva equivalent"* measure, the pool contained 100 grams wet weight of green alga; replicate determinations and extrapolations were within 9 grams of the mean. This reduced to 30 grams dry weight and 15 grams of organic matter. The two algal species had an estimated standing crop of 62 grams of organic matter, which, with 3.5 grams of seston, compared with 170 grams of consumer. This was indeed an inverse Eltonian pyramid and startled the class which by this time had been subjected to classical theory!

The project was forced into its last phase, a consideration of production. Estimates were made of green algal production by the light and dark bottle method. Based on an average photosynthetic day, these determinations gave a figure of 310 mg organic production per gram dry weight, a turnover every 3 days. The known carbon fixation of the coralline is much less, nearer 3%. Together, these 2 algal species produce 23 grams of organic matter daily or a staggering annual production of 8,395 grams. Comparison with the 170 grams animal standing crop, gave us a more proper pyramid. But to complete the ledger, consumer standing crop had to be converted to production.

Here our project ended and OLP would never take its place with Cedar Bog lake, Eniwetok, or Georges Bank! Growth data and physiological information were not available for our array of animals. Unsuccessful attempts were made to measure growth by morphometric studies on two of the snails. With our "purish" attitude, we did not attempt an estimate of turnover rates. Nor did we know the energy loss in respiration, in feces, or by the daily flushing of uneaten animal and algal materials. The crowning example of ignorance came when algologist G. J. Hollenberg doubted, after culturing our green alga, that it was a known species; he placed it in the family Chaetophoraceae.

In Retrospect

We were impressed with these values of such a microcosm approach in a class study of community ecology:

1. Untrained students were exposed to many techniques in a meaningful field context; on several occasions new methods were devised.
2. Many basic ecological concepts, developed in other facets of the course, were corroborated and intriguing new leads were recognized.
3. Field and laboratory approaches were seen to be necessarily complimentary.
4. Accuracy and replication of measurement were stressed, but so also was the natural history approach with its virtues of quiet and prolonged observation.
5. While pleased with the progress of the study, the class was continuously reminded of the complexities of ecological relationships, of how little is known of many of the more common species, and of how imperative it would be to make year-round studies. They achieved a certain ecological humility, and a respect for and reservations concerning the mounting number of works on larger ecosystems, some of which they had read.
6. The project, while conceived by the instructors, was allowed to develop with a minimum of direction even to the point of mistakes and meaningless tacks; the class was experiencing research.
7. By far the greatest value derived from the microcosm approach was the holistic view, the ability of the student to have a picture of the whole at all times and there-

fore, a more meaningful appreciation of the structure and forces maintaining that whole.

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SATURATED SOLUTIONS FOR THE CONTROL OF HUMIDITY IN BIOLOGICAL RESEARCH[1]

INTRODUCTION

The control of humidity in small closed spaces has become increasingly important in the last 30 years to ecologists and physiologists working with small animals, especially arthropods. This factor is often so important in the ecology and physiology of the organisms that it is a variable which must be under careful control. We have been using saturated salts successfully for this purpose for several years and have been urged by other workers to publish the extensive information which is available on this method in a journal easily accessible to biologists. The following lists of saturated solutions and humidities, gathered primarily from the literature, are quite complete and should provide a good range of conditions for ecological and physiological work. Data of this sort have been incomplete and inadequate in the biological literature (Buxton and Mellanby 1934 and Solomon 1951), and most of the recent material has been published in chemical and trade journals which are not commonly used by biologists (*cf.* O'Brien 1948, Wink and Sears 1950, Richardson and Malthus 1955). Many of the relative humidity values presented in earlier works (*e.g.* Sweetman 1933, Janisch 1938) are not accurate because of the use of impure salts and questionable methods. For excellent discussions of the basic concepts and problems of humidity, vapor pressure, etc., the reader is referred to Buxton (1931), Edney (1957), and Beament (1958).

Solutions maintain constant relative humidities in the atmosphere over them because any water solution of a non-volatile substance will have a definite water vapor pressure at a given temperature when the vapor phase is in equilibrium with the liquid. The constancy of the vapor pressure can be explained further by use of the Gibbs Phase Rule discussed in texts of physical chemistry. Saturated solutions with an excess of solids (the "supersaturated solutions" of some earlier authors) maintain a very constant vapor pressure even under changing moisture conditions because a gain of water causes some of the solid to go into solution and a loss of water causes some of the dissolved material to precipitate. As long as there is not so much liquid over the solid that diffusion within the solution is too slow, the humidity conditions will remain unchanged. Thus, considerable amounts of water can be gained or lost by the organism without changing the vapor pressure.

We have found saturated salts more satisfactory for maintaining constant relative humidities than various concentrations of KOH, H_2SO_4, and other substances as proposed by Solomon (1951) and others. These solutions do not change in vapor pressure as much with temperature changes and one can set up desired series of humidities easily, but once these solutions have gained or lost water their vapor pressure will have changed and they must be discarded. Also, the frequent determinations of concentrations becomes time-consuming and tedious. The saturated solutions may be kept for long periods, and repeated or prolonged use does not alter their vapor pressures as long as they are handled with reasonable care.

We have also included several methods for testing the R. H. over these solutions which have proven satisfactory in this and other laboratories. These will be useful to workers who need to extend the information presented in this paper and to determine the relative humidity in any closed space where control is not possible or desired.

SATURATED SOLUTIONS

The saturated solutions presented in Table I will produce satisfactory results if certain precautions are observed. A closed container must be used and anything over one liter in volume should be provided with a device for keeping the air in motion. As large a surface of the solution as possible should be exposed to allow for free diffusion of water. Reagent grade chemicals should be used at all times to allow for reproduceability, and the solutions can be used repeatedly as long as they do not become contaminated. The solutions are prepared by dissolving enough solid to saturate at boiling and allowing this to partially cool, at which time a small amount of solid should be added. After the mixture has cooled, considerably more solid should be added and this allowed to stand for from several days to a week to insure saturation. KBr and potassium acetate ("KAc" in our formula) may take even longer; 2 to 3 weeks is not too long to wait before use. If the solution is saturated with an excess of salts at boiling, a solid mass will result when it cools; this wastes salts and is difficult to remedy.

The temperature of the system must be kept constant with a well-controlled water-bath. However, certain salts, such as NaCl, are quite consistent over a wide range of temperatures (see Table I) and choice of one of these would reduce the error introduced by temperature fluctuations. Very hygroscopic substances, especially those producing low humidities, should be used as a sludge made up of solid and a small amount of saturated liquid. These will take up water rapidly and it is possible to have a layer of unsaturated liquid on the surface if there is too much liquid initially. This is especially important when two solutions are used to set up a gradient; the solution with the lower vapor pressure must be in the form of a sludge as it will be constantly gaining water; while that with the higher v.p. must have rela-

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[1] The research in which this was used has been supported in part by a grant from the Council on Research and Creative Work of the University of Colorado.

TABLE I. Relative humidity values over saturated solutions at various temperatures

Temperature °C	2°	5°	10°	15°	20°	25°	30°	35°	40°	45°	50°
Compound											
NH_4Cl	....	....	79.0	79.5	79.5	78.0	77.5	....	74.0	....	71.5
NH_4HPO_4 (monophosphate)	....	....	....	....	93.0	93.0	92.0	....	91.0	....	....
NH_4NO_3	....	....	75.0	70.0	65.5	62.5	59.5	55.0	53.0	50.5	48.0
$NH_4NO_3 + NaNO_3$	....	....	58.0	55.0	52.0	50.0	47.0	44.5	42.0	39.5	36.5
$NH_4NO_3 + AgNO_3$	....	....	70.5	68.0	65.1	61.5	58.0	55.0	52.0	48.5	44.5
$(NH_4)_2SO_4$	*0°* 83.5	82.5	80.5	81.0	80.5	80.0	80.0	79.5	79.0	79.0	78.0
$CaCl_2 \cdot 6H_2O$[1]	....	40.0	38.0	35.0	32.5	29.5	....	....	....	....	....
$CaHPO_4 \cdot 2H_2O$[2]	....	....	97.5	99.5	95.0	97.0	95.0	....	95.5	....	95.0
$CaH_4(PO_4)_2 \cdot H_2O$[3]	....	....	98.0	99.0	94.0	96.0	93.5	....	94.5	....	94.5
$Ca(NO_3)_2 \cdot 4H_2O$[4]	*0°* 66.0	....	....	56.0	55.5	50.5	47.0	....	(36.0)	....	...
$CoCl_2$[5]	....	....	....	*18°* 72.5	67.0	....	62.0	....	56.5	....	....
Cr_2O_3[6]	....	....	....	45.5	(39.0)	....	44.5	....	45.0	....	45.5
Glucose	(60.0)	....	*12°* 57.0	....	55.0	55.0	....	55.0	....	....	....
$LiCl \cdot H_2O$[7]	*0°* 14.5	14.0	13.5	13.0	12.5	12.0	11.5	11.5	11.0	11.0	11.0
$Pb(NO_3)_2$[8]	....	....	98.0	97.0	97.0	95.5	95.0	94.5	94.5	94.0	92.5
$Pb(NO_3)_2 + NH_4NO_3$	....	....	66.5	62.0	58.0	55.0	52.5	49.5	47.0	44.5	41.5
$MgCl_2 \cdot 6H_2O$	*0°* 35.0	34.5	34.0	34.0	33.0	32.5	32.5	32.5	32.0	31.5	31.5
$Mg(NO_3)_2 \cdot 6H_2O$	60.5	59.0	58.0	56.0	55.0	53.0	52.0	50.5	49.0	47.5	46.0
P_2O_5	00.0	....	00.0	00.0	00.0	00.0	00.0	....	00.0	....	00.0
KAc	(23.5)	....	(21.0)	....	20.0	22.5	22.0	....	20.0	....	....
KBr	....	....	86.0	....	84.0	80.0	82.0	....	79.5	....	79.0
$K_2CO_3 \cdot 2H_2O$[9]	47.0	....	47.0	44.0	44.0	43.0	43.5	....	40.0	....	....
KCl	(88.0)	....	88.0	86.5	85.0	85.0	84.5	83.0	82.0	81.0	80.5
K_2CrO_4	....	....	....	....	88.0	....	86.5	....	85.5	....	....
$K_2Cr_2O_7$	....	....	....	....	98.0	98.0	97.5	96.5	96.0	....	95.5
KH_2PO_4	....	....	98.0	99.0	96.5	96.0	93.5	....	93.0	....	92.5
$KF \cdot 2H_2O$[10]	....	....	....	....	....	30.5	27.4	....	23.0	....	20.5
KNO_3[11]	*0°* 97.5	96.5	96.0	95.5	93.5	92.5	91.0	89.5	88.0	86.5	85.0
KNO_2	....	....	....	....	48.5	....	47.0	....	46.0	....	....
K_2SO_4	99.0	98.5	98.5	99.0	98.0	97.5	96.5	96.0	96.5	96.0	96.0
KCNS[12]	....	....	52.0	50.0	47.0	46.5	43.5	41.5	41.0	38.0	36.5
K Tartrate[13]	....	....	....	75.0	75.0	75.0	74.0	....	74.0	....	....
KNa Tartrate[14]	....	....	87.5	....	87.0	87.0	87.0	....	86.0	....	....
Pyrocatechol	....	....	....	99.0	95.5	93.5	92.5	90.5	88.0	85.0	81.5
Resorcinol	....	....	....	95.0	87.0	85.0	82.5	79.5	76.0	72.5	68.5
$AgNO_3$	....	....	88.0	86.0	84.0	82.0	80.0	78.0	76.5	74.5	72.0
$AgNO_3 + Pb(NO_3)_2$	....	....	84.0	83.0	80.5	78.5	76.5	75.0	73.0	71.0	69.0
$NaAc \cdot 3H_2O$	....	....	....	....	75.0	73.0	71.5	....	67.0	....	....
$NaBr \cdot 2H_2O$[5]	....	....	63.0	61.0	59.0	57.5	56.0	54.5	53.0	51.5	49.5
$Na_2CO_3 \cdot 10H_2O$[16]	....	....	(99.0)	....	92.0	87.0	87.0	....	....	....	....
NaCl	*0°* 75.0	75.0	76.5	76.0	76.0	75.5	75.5	75.5	75.0	75.0	74.5
NaCl + KCl	....	....	....	....	70.0	71.5	71.0	....	....	....	....
$Na_2CrO_4 \cdot 4H_2O$	....	....	....	....	....	....	64.5	....	62.0	....	58.0
$Na_2Cr_2O_7 \cdot H_2O$[17]	60.5	59.5	60.0	56.5	54.5	53.0	52.5	51.0	50.0	48.5	47.0
NaOH	(5.5)	....	(5.5)	....	5.5	7.0	(4.0)	....	(1.5)	....	....
NaI	....	....	....	....	38.0	38.0	36.0	....	32.5	....	29.0
$NaNO_3$	....	....	77.5	76.5	76.0	74.0	72.5	71.0	70.5	68.5	67.5
$NaNO_2$	....	....	....	....	65.5	64.0	63.0	....	61.5	....	60.0
$Na_2SO_4 \cdot 10H_2O$	....	....	....	....	(93.0)	(93.0)	....	(87.0)	(88.5)	....	(88.5)
Na tartrate[18]	....	....	....	94.0	92.0	92.0	92.0	....	92.0	....	....
Urea	....	....	81.5	80.0	8.0	76.0	73.3	....	68.5	....	62.5
$ZnCl_2 \cdot 1\frac{1}{2}H_2O$[19]	(10.0)	(10.0)	(10.0)	(10.0)	10.0	....	(10.0)	....	(10.0)	....	10.0
$ZnSO_4 \cdot 7H_2O$[20]	....	94.5	....	....	....	88.5	....	....	84.0	...	....

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[1] May be unstable around 20° C.
[2] May be a transition point between 15° and 20°.
[3] Calcium monophosphate.
[4] Good up to 42°.
[5] Uncertain around 20°, large temperature coefficient.
[6] Wink and Sears (1950) have lower values (40%) at 30° and 40°.
[7] $LiCl.XH_2O \longrightarrow LiCl.H_2O$ at 12.5°.
[8] Solution slightly acid due to hydrolysis, but stable.
[9] Should be granulated then moistened; powdered form is unstable.
[10] $KF.2H_2O \longrightarrow KF$ at 50°.
[11] Large temperature coefficient.
[12] Very toxic.
[13] Potassium tartrate. Excellent.
[14] Potassium sodium tartrate (Rochelle Salts). Good only below 40°.
[15] Good up to 55°, large temperature coefficient.
[16] $Na_2CO_3.10H_2O \ldots\ldots > Na_2CO_3.H_2O$ at 32°.
[17] Very good; small temperature coefficient.
[18] This is also listed with one water of hydration, instead of two; good only below 40°.
[19] Unstable around 20°.
[20] Good below 40°.

tively more liquid and less solid as it will be losing water.

Mixtures of 2 or more salts must be used cautiously (Richardson and Malthus 1955) and only those with cations or anions common to both salts give consistent results; when all 4 components are different one cannot tell which solids are forming. Also, with most mixtures of salts with common ions there will be interaction between them to form complex radicals and the resulting vapor pressure will not represent the simple addition of the pressures over the individual salts. Thus, the reader is cautioned to measure the vapor pressure at temperatures for which values have not been published; interpolation is not recommended. The solutions should be made up separately and then combined; otherwise, there is no way to determine which is forming a precipitate. The ratios of the 2 salts are unimportant as long as both are saturated (Dingemans 1946), though it seems that an approximate one to one mixture would be advisable. If too small an amount of one salt is used, the addition of water may dissolve its solids and the solution would not then be saturated with respect to this salt.

Certain salts are unsuitable because of instability or irregular behavior. Richardson and Malthus (1955) list several halides ($FeCl_3$, $AlBr_3$, $AlCl_3$, and $ThCl_4$) that are prone to hydrolysis, and certain other halides are known to be light-sensitive. $FeCl_3$ with an R. H. of 5.0% at 25° is the only one of the former that might be used to good advantage despite the difference between preparations. Buxton and Mellanby (1934) indicate that NH_4Cl releases traces of NH_3 and that LiCl gives off Cl_2 above 37°.

Certain salts have transition points within the range considered and these have been indicated in Table I. This is usually the loss of some or all the water of hydration as the temperature rises, e.g. $Ca(NO_3)_2.4H_2O \rightarrow Ca(NO_3)_2$ at about 42°. It is important that these transition points be known because salts should not be used at or close to the critical temperature and because one cannot safely interpolate the values on a curve around or above that temperature. Estimation of humidity values must be used cautiously unless the characteristics of the salt are well known as is the case with $Pb(NO^8)_2$ which has R.H. values that fall on a very straight line over a wide range of temperatures (Dingemans 1945). Carr and Harris (1949) found no transition points for the following salts between 15° and 50°: NaCl, HCl, KBr, KI, $NaNo_3$, $NaNO_2$, CrO_3, and KF. Certain salts are noted as having large temperature coefficients which means that the solubilities, and thus the R.H., will change considerably with changes in temperature. One must be careful that a solution is stirred and allowed ample time to come to equilibrium when its temperature is changed or the surface liquid may not become saturated.

In Table I salts are listed with R.H. values for temperatures at which they are known. One value only is given, simply to avoid the confusion which would result from a complete listing of all published values. In the many cases in which 2 to 10 values have been published, we averaged those that were clustered around a point; those far away from the average were ignored. The averages were rounded to the nearest half percentage point; biological work with humidities seldom requires anything more exact than this though reagent grade chemicals should still be used. The choice of salts should be governed by cost, availability, and reproduceability of results; there are several from which to choose at most humidities and temperatures. Superscripts indicate notes concerning such matters as transition points, and temperatures other than those at the head of the columns are included above the R.H. values. References have been omitted from the table because of their large number and the combining of so many of the values, but entries in the bibliography from which these values were obtained are starred. Table II includes those chemicals for which only one or two R.H. values are known to the authors. R.H. values which are in parentheses in both tables have had some doubt expressed on their accuracy in the literature.

TABLE II. Relative humidity values over saturated solutions at given temperatures

	R. H.		R. H.
At 20° C.			
$BaI_2 \cdot 2H_2O$	44.0	$NaHSO_4$	52.0
$CaSO_4 \cdot 2H_2O$	98.0	$NaBrO_3$	92.0
$Mg(Ac)_2 \cdot 4H_2O$	65.0	$NaNO_3 + KNO_3$	71.0
$MgSO_4 \cdot 7H_2O$	90.0	$Na_2HPO_4 \cdot 7H_2O$	95.0
$MnCl_2 \cdot 4H_2O$	57.5	Na_2SO_3[21]	95.0
$NiCl_2 \cdot 6H_2O$	55.5	NaCNS	35.5
H_3PO_4	9.0	$Na_2S_2O_3$	78.0
$KHSO_4$	86.0	$Zn(NO_3)_2$	42.0
K_2HPO_4	44.5		
At 25° C.			
NH_4Br_2	75.0	$MgSO_4 \cdot 7H_2O$	89.0
$BaBr_2$	74.5	$Mg(CNS)_2$	47.5
$BaCl_2$	90.0	$MnBr_2 \cdot 6H_2O$	34.5
$BaI_2 \cdot 2H_2O$	43.0	$MnCl_2 \cdot 4H_2O$	56.0
$Ba(CNS)_2 \cdot 2H_2O$	54.5	$NiBr_2 \cdot 3H_2O$	27.0
$CaAc_2 \cdot H_2O$	17.0	$NiCl_2 \cdot 6H_2O$	53.0
$CaAc_2 \cdot H_2O$ + sucrose	13.0	H_3PO_4	9.0
$CaBr_2$	16.5	KBr + sucrose	63.0
$CaI_2 \cdot 6H_2O$[22]	11.5	KBr + urea	51.0
Ca methane sulphonate	72.5	$KClO_3$	98.0
$Ca(MnO_4)_2 \cdot 4H_2O$	37.5	$KCl + KClO_3$	85.0
$Ca(CNS)_2 \cdot 3H_2O$	17.5	$KHCO_2$ (Formate)	21.5
$CaZnCl_2$[23]	20.0	KOH	8.0
$CeCl_3$ (tech.)	45.5	$K_4P_2O_7 \cdot 3H_2O$	49.5
$CrCl_3$	42.5	$K^2S_2O_3$	66.0
$CoBr_2$	41.5	NaAc + sucrose	57.0
$Co(NO_3)_2 \cdot 6H_2O$	(49.0)	NaCl + sucrose	63.0
$CuBr_2$	62.5	$NaCl + NaNO_3$	69.0
$CuCl_2 \cdot 2H_2O$	67.0	$NaCl + Na_2SO_4 \cdot 7H_2O$	74.0
$Cu(NO_3)_2 \cdot 6H_2O$	(35.0)	NaH_2PO_4	81.0
Ethanolamine sulphate	12.5	Na methane sulphonate	70.0
$FeBr_2 \cdot 6H_2O$	39.0	$NaMnO_4 \cdot 3H_2O$	61.5
$FeCl_2 \cdot 4H_2O$	60.0	$SrBr_2 \cdot 6H_2O$	58.5
$LaCl_3 \cdot 7H_2O$	47.0	$SrCl_2 \cdot 6H_2O$	71.0
$LiBr \cdot 2H_2O$	7.0	$SrI_2 \cdot 6H_2O$	33.0
$LiI \cdot 3H_2O$	18.0	$Sr(CNS)_2 \cdot 3H_2O$	31.5
$LiNO_3 \cdot 3H_2O$	47.0	Sucrose	85.0
LiCNS[22]	12.5	Sucrose + urea	52.0
$MgBr_2 \cdot 6H_2O$	31.5	$ZnBr_2$	8.5
MgI_2[22]	27.0	ZnI_2[22]	20.0
$Mg(ClO_4)_2 \cdot 6H_2O$	(41.0)	$Zn(MnO_4)_2 \cdot 6H_2O$	51.0
Mg silicofluoride	91.5	$Zn(CNS)_2$	80.5

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[21] Good only below 29.6°.
[22] Light sensitive.
[23] Prepare by mixing $Ca(OH)_2 + ZnO + 4HCl$.

Drying agents are so important for attaining very low humidities that a table has been included from the International Critical Tables (Shepherd 1928) showing the relative efficiency of drying agents known at that time. The solid desiccants should be used with caution, however,

Table III. The efficiency of drying agents

Compound	Mg. of H_2O remaining/liter of gas dried at 25°.
P_2O_5	$<2 \times 10^{-3}$
$Mg(ClO_4)_2$	$<5 \times 10^{-4}$
$Mg(ClO_4)_2 \cdot 3H_2O$	$<2 \times 10^{-5}$
KOH (fused)	0.002
Al_2O_3	0.003
H_2SO_4	0.003
MgO	0.008
NaOH (fused)	0.16
$CaBr_2$	0.2
CaO	0.2
$CaCl_2$	0.14–0.25
H_2SO_4 (95%)	0.3
$CaCl_2$ (fused)	0.36
$ZnCl_2$	0.8 (=3.2% R. H.)
$ZnBr_2$	1.1
$CuSO_4$	1.4

for a layer of saturated solution can form over the surfaces of the particles and cut down their efficiency if there is much water present initially. To change the figures in Table III to relative humidity, substitute in the following equation which has been derived by using the gas constant and reducing conditions to standard volumes and pressure. R.H. = 3.98W, where W is the weight (in mg) of water in a liter of gas at 25°C.

Determination of Relative Humidity

Numerous methods for testing relative humidity in small, closed spaces have been presented in the literature and all have advantages and disadvantages for use by the biologist. Reasonable to very accurate results may be obtained with the dew-point hygrometer (see below), manometric methods measuring vapor pressure directly (Buxton and Mellanby 1934), certain of the electric hygrometers which measure the changes in conductivity of hygroscopic substances (Edney 1953, Van Kuijgek 1955, and the American Instrument Co.), and the isopeistic method to be described below.

There are also less accurate methods which will frequently serve one's purposes quite well. Hair hygrometers (Buxton and Mellanby 1934) are limited to relatively large spaces and need to be calibrated carefully and frequently. The $CoCl_2$ system of colored papers (Solomon 1951) has proved to be very unsatisfactory in this laboratory because the papers are very difficult to prepare with any accuracy, the color changes are not sharp, and standards must be kept under mineral oil which changes the colors drastically. Dessens (1946) describes a method by which the R.H. can be estimated by changes in the diameter of drops of LiCl solutions. Ludwig and Anderson (1942) adapted a suggestion by Buxton (1931) using the gain in weight of an hygroscopic organic material. They dried small (50 mg) pieces of gelatin to constant weight and then calibrated these over known solutions of KOH (see below). This method is quite good at the higher humidities but is not as accurate at the very low ones. However, a simple method proposed by Pouncey and Summers (1939) has been very useful to us in checking gradients in small spaces though its accuracy is limited.

This method utilizes the fact that a salt crystal will pick up moisture and deliquesce in humidities which are at or above that maintained by its saturated solution. A very small crystal is introduced into the closed chamber and observed under magnification. If the R.H. is below that for the salt, there will be no change; if it is above, the crystal will liquefy quite rapidly. However, if the R.H. is very close, the deliquescence will be only partial; if a bit lower, the surface will become smooth and shiny; if just above, there will be a narrow rim of liquid around the mass. We have found this method effective despite the limitations in accuracy though one does need a large number of salts from which to choose.

We have found that R. H. determinations by the dew-point method require considerable operator-judgment of the end-point of condensation which is not sharp but rather a progressive phenomenon. Since the coolant is ether which penetrates most materials commonly used to seal openings, glass, metals, and "Teflon" are the only satisfactory materials with which to keep the ether confined. It is, of course, imperative that no ether leak into the test chamber. The air in this test chamber can be maintained at the desired temperature only by using a large water bath, adequate stirrers, and an accurate thermostat. The test chamber must also be relatively large to prevent the cooling of the condensation chamber from influencing the temperature of the solution and the air above it. In this laboratory satisfactory results were obtained only after many trial and error observations and the use of an arbitrary end-point of condensation.

The most accurate, yet relatively simple, system for the determination of R.H. was developed by Robinson and Sinclair (1934) and is called the isopeistic method. This has been adapted and described by Richardson and Malthus (1955) and reference to their paper may be made for additional information not included in the following description. This method utilizes a reference solution (H_2SO_4 and others listed below) of known molal concentration which is allowed to come into equilibrium with the saturated solution in a closed container. The change in weight of the reference solution is then measured, from which the R.H. in the chamber may be found. This method seems to allow less chance for error and reliance on judgment than do others.

The two solutions are placed in small dishes of hard glass fitted with tight, but easily removable, covers. Equilibrium is attained much more rapidly if the chamber is evacuated to about 10 mm Hg pressure. Sputtering of H_2SO_4 when the pressure is lowered can be prevented with acid-washed glass wool. The salt should be in the form of a sludge for these tests. The vacuum is broken with dry air and the covers replaced as rapidly as possible. The chamber should be kept in a constant temperature bath and a gentle rocking motion applied to it to insure equilibrium. When the reference solution has reached constant weight in one to several days the R.H. can be found from one of the isopeistic tables listed in Table IV. Initially, the molality of the reference solution should be as close as possible to that which will give the expected R.H. value for the salt; this will shorten the time it takes to reach equilibrium.

Summary

1. Tables are presented which give the relative humidity over the saturated solutions of nearly one hundred substances. The use of these saturated solutions for the control of humidity in small, closed spaces is explained as are the advantages and disadvantages of this and other methods.

2. A number of methods for the measurement of hu-

TABLE IV. Sources of vapor pressure values for the isopeistic method

Compound	Range (% R. H.)	Reference
Glycerol	0-100	Braun and Braun, 1958
KOH	10-90	Buxton and Mellanby, 1934
H_2SO_4	20-90	
H_2SO_4	5.4-92	Shankman and Gordon, 1939
KCl	84-99.7	Stokes and Levien, 1946
NaCl	76-99.6	
H_2SO_4	29-85	Stokes, 1947
NaOH	29-79	
$CaCl_2$	75.0	
NaCl	77-85	
KOH	14-100	Solomon, 1951
H_2SO_4	5-100	
$CaCl_2$	5-95	Stokes and Robinson, 1951
H_2SO_4	5-95	
NaOH	5-95	

midity are explained both with an emphasis on accuracy and on ease and convenience for use.

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* Note: Starred entries contain relative humidity values over saturated salts.

TESTS OF RANDOMNESS IN RECAPTURES OF *RANA P. PRETIOSA*[1]

INTRODUCTION

Of various indirect methods of determining animal numbers, no technique has been so widely utilized as the Lincoln or proportional index method. The assumptions on which this method is based are regularly recited by various authors as a prologue to studies of population size based on this technique, but it has been only recently that attention has been turned to the question of how well these assumptions are actually fulfilled in nature. For example, one may ask, following a marking program, whether both marked and unmarked animals are equally susceptible to subsequent capture. The work of Chitty & Kempson (1949) and Leslie, Chitty & Chitty (1953) with small rodents (especially *Microtus agrestis*) has demonstrated that because of an initial reluctance of unmarked animals to enter a trap, a marked animal is more susceptible to recapture than an unmarked one to capture (for another view see Brown 1954). Pearson (1955) found that marked and unmarked spadefoot toads were not equally susceptible to capture because of periodic activity and quiescence on the part of various subgroups of the population.

A related question is whether recaptures among *marked* animals are random. In this case, Leslie, Chitty & Chitty found that once voles had been trapped and marked, recaptures among the marked cohort were at random. On the other hand, Orians (1958) has demonstrated that recaptures among shearwaters (*Procellaria puffinus*) marked on Skokholm Island are not random. Orians also comments on non-randomness of recaptures in alpine swifts (*Apus melba*) in the course of a study by Arn (treated statistically by Hammersley 1953). It is important, however, to distinguish between *this* kind of non-randomness (*i.e.* with the swifts), which was caused by deliberately non-random collecting effort, and non-randomness caused by behavioral differences among marked animals, when the investigator has adopted a sampling procedure that would be expected to result in random captures. However, in either case, if it is established that recaptures among marked animals of a population are not random, the use of the proportional index method to estimate population size is not valid. The importance of testing the assumption of randomness of recaptures when possible is then evident.

It is the purpose of this paper to present data pertaining to recaptures of marked frogs in a population of the western spotted frog, *Rana p. pretiosa*, in Yellowstone Park, Wyoming. This inquiry was suggested by the statistical appendix prepared by Leslie (1958) for Orians' paper on shearwaters and on which Orians' conclusions were, in part, based. The advice of Dr. David DeForest of the Department of Biology, Wayne State University, is gratefully acknowledged.

PROCEDURE

Leslie (1958) points out that in testing for randomness of recaptures among marked individuals, one may examine a selected cohort of marked animals known to be alive, and hence presumably at risk, over a time interval during which a number of censuses were made. From the number of marked individuals in the cohort captured in successive samplings, one may establish a series of probabilities of recaptures at each of the successive samplings, *e.g.* p_1, p_2, p_3, etc. Then by setting q_t $(= 1 - p_t;\ t = 1, 2, 3\ .\ .\ .\ .\ n)$, and expanding $(p_1 + q_1)$ $(p_2 + q_2)$ $(p_3 + q_3)\ .\ .\ .\ .\ (p_n + q_n)$, one may calculate the expected frequency distribution of recaptures assuming that all individuals are recaptured at random. If $p_1 = p_2 = p_3 = p_n$, the expansion is according to the binominal distribution but in practice this is not apt to occur unless by design. Leslie observes that this system is apt to involve laborious computations if the data are extensive and suggests a shorter method, basically that of comparing the calculated and expected variances of the observed frequency distribution and testing for significant difference. The reader is referred to Leslie's paper for a fuller account of both methods.

The following involves an application of both methods, as outlined above. The data are drawn from a 3-year study of frogs. The hypothesis that marked frogs are recaptured at random is adopted and the following tests performed to test this assumption.

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[1] Contribution No. 34 from the Department of Biology, Wayne State University, Detroit, Michigan.

Five subpopulations of marked animals have been analyzed and the preliminary data are set forth in Table I. The first 4 groups were censused over periods of time ranging from 2 to 4 weeks. The fifth group, of 86 frogs, has been treated in a somewhat different manner. In the course of the 3-year study, 297 frogs were marked during the summer of 1953. Of these, 86 were alive in 1955 or in September of 1954 (as evidenced by recaptures). Then these 86 frogs were presumably available for recapture during the summer of 1954. If the summer of 1954 is divided into 3 periods (May 23 to June 15, June 16 to July 9, and July 10 to September 20), the recaptures of the 86 frogs within these 3 intervals may be recorded. If a frog was recaptured more than once within any one time interval, only one recapture has been counted. Thus, during 1954, any one of these 86 individuals might have been recaptured not at all, once, twice, or 3 times.

TABLE I. Recaptures of marked *Rana p. pretiosa*

	FRACTION OF TOTAL COHORT RECAPTURED AT EACH CENSUS						
Cohort size	1	2	3	4	5	6	7
20.........	2 (0.1)	4 (0.2)	4 (0.2)	2 (0.1)	4 (0.2)	6 (0.3)	7 (0.35)
20.........	3 (0.15)	9 (0.45)	5 (0.25)	3 (0.15)	6 (0.3)	2 (0.1)	
24.........	14 (0.58)	5 (0.21)	9 (0.38)	7 (0.29)	13 (0.54)	8 (0.33)	
40.........	3 (0.075)	5 (0.125)	9 (0.225)	28 (0.7)			
86.........	28 (0.33)	34 (0.40)	27 (0.31)				

Table II shows, for each of the 5 groups, the expected frequency distributions based on data in Table I, the observed frequency distributions and the χ^2 totals (with 3 degrees of freedom in each case). For these values of χ^2, the probabilities that the observed frequency distributions agree with random expectations range from 0.4 to 0.9.

Table III shows the results of a comparison of the theoretical variance (as calculated from the various values of p and q in Table I, $\sigma^2 = \Sigma p_t q_t$). The values for $\sqrt{2\chi^2} - \sqrt{2\text{d.f.} - 1}$ are presumed to be distributed normally about zero with unit variance (see Leslie 1958) and the values for P are obtained accordingly.

TABLE II. Comparison of expected and observed frequency distributions in recaptures of marked *Rana p. pretiosa*

Cohort size	Number of times recaptured	Chance of reacpture (p)	Expected on basis of cohort size	Observed	χ^2
20	3-7	.17	3.4	2	.58
	2	.27	5.4	6	.07
	1	.37	7.4	8	.05
	0	.19	3.8	4	.01
	Totals	1.00	20.0	20	.71
20	3-6	.14	2.8	4	.51
	2	.29	5.8	3	1.34
	1	.38	7.6	7	.05
	0	.19	3.8	6	1.27
	Totals	1.00	20.0	20	3.17
24	4-6	.15	3.6	4	.04
	3	.27	6.5	7	.04
	2	.33	7.9	6	.46
	0-1	.25	6.0	7	.17
	Totals	1.00	24.0	24	.71
40	3-4	.03	1.2	2	.53
	2	.23	9.2	9	.00
	1	.55	22.0	20	.18
	0	.19	7.6	9	.26
	Totals	1.00	40.0	40	.97
86	3	.04	3.4	4	.11
	2	.23	19.8	21	.07
	1	.45	38.7	35	.35
	0	.28	24.1	26	.15
	Totals	1.00	86.0	86	.68

TABLE III. Comparison of expected and observed variances of frequency distributions of recaptures of marked *Rana p. pretiosa*

Cohort size	Number of censuses	Total number of recaptures	Mean of frequency distribution (μ)	Theoretical variance (σ^2)	Sum of squared deviations $(x - \mu)^2$	$\frac{(x-\mu)^2}{\sigma^2}$ (X^2 of Leslie)	$\sqrt{2X^2} - \sqrt{2\text{d.f.} - 1}$ (assuming $X^2 = \chi^2$)	Probability of greater difference than observed
20	7	29	1.450	1.098	34.95	31.85	1.90	.057
20	6	28	1.400	0.990	38.80	39.19	2.77	.006
24	6	56	2.333	1.320	43.33	32.83	1.39	.165
40	4	45	1.125	0.563	30.38	53.95	1.62	.105
86	3	89	1.035	0.674	62.77	93.13	0.57	.569

DISCUSSION

Of the 5 groups of frogs tested, none shows cause for rejecting the initial hypothesis on the basis of the tests represented in Table II. However, when the more sensitive tests advocated by Leslie are employed (Table III), the probabilities of the observed distributions representing random expectations are low except when N = 86. On the other hand, if one adopts a value of $P < .05$ as cause for rejection of the hypothesis, one would accept the hypothesis except where $P = .006$.

The comparison of the theoretical and observed variances is much less taxing, in terms of calculations, than the other method and is a more rigorous test. Nevertheless, in some cases, the calculation of the expected frequency distribution may direct attention to the cause of non-randomness. No explanation is tendered for the apparent lack of random recaptures in one of the groups analyzed, but it may be seen in this distribution, and the others, that there were more frogs not recaptured at all than expected. This was also true among the shearwaters analyzed by Leslie (1958), where it appeared that some of the birds, although alive, were not actually available for recapture. A similar situation might have existed in the groups of frogs tested.

In view of the findings with regard to some small mammals and birds, which suggest that one or more of the fundamental assumptions of the proportional index technique may not be fulfilled, it is reassuring to have some indication that the assumption of randomness in recaptures of marked frogs is justified. Jameson (1955), Martof (1956), Pyburn (1958), and Turner (1959) have all employed the proportional index method for estimating numbers of anurans, and, while it is likely that certain other assumptions were not always fulfilled in their work, we now have some evidence to suggest that lack of randomness in recaptures of marked animals was not a problem.

In conclusion, it should be stressed that the foregoing tests apply only to the recapture of marked animals and give no assurance that recaptures among both marked and unmarked animals are at random—another assumption of at least equal importance. However, my experience suggests that capture and marking does not modify the behavior of anurans and it seems likely that the assumption of random captures may be extended to the whole population at risk, *i.e.* both marked and unmarked individuals.

SUMMARY

The hypothesis that marked frogs in 5 subpopulations of *Rana p. pretiosa* (N ranging from 20 to 86) were recaptured at random was tested as advocated by Leslie (1958). Comparisons of observed and expected frequency distributions gave no cause for rejection of the hypothesis. Comparisons of observed and expected variances of distributions gave, in 4 cases, low probabilities of randomness (.006 to .165) but cause for rejection ($P < .05$) in only one case.

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REVIEWS

The Study of Population[1]

This imposing volume bears a title to excite ecologists and the dust jacket asserts that "it is the most thorough and sophisticated appraisal to date . . . and will be a standard reference work for years to come." Obviously, someone must appraise it for the readers of Ecology. At the behest of the Review Editor I have struggled at least once through every page and am now ready to report. This will center about 3 conclusions as follows: (1) there is relatively little in this volume for ecologists, (2) in large part it is an extremely dull book, and (3) a wide and deep chasm seems to separate plant and animal ecologists from those who designate themselves as "human ecologists" and "demographers."

The Cold Spring Harbor Symposium on Population Studies was held in June, 1957 by which time, apparently, the contributions to the present symposium had already been written. There is no reference here to the earlier CSH volume which, unlike the present publication, is oriented toward the biologist.

The plan of this compendium is simple enough. The editors have most of their say in the largely synoptic 120 pages of Part I. Next come a couple of hundred pages dealing with the history and current status of demography in various parts of the world. Part III contains 12 chapters averaging 25 pages each on such "elements of demography" as "fertility," "mortality," "family statistics," and "working force." The final section deals with the relations between population studies and "other fields" such as ecology, genetics, "human ecology," and economics. In all, 28 contributors appear, and I personally found something under one-third of the 33 chapters to be worth the often considerable difficulty of reading and understanding them.

Lorimer's chapter on the history of demography is a scholarly contribution and I was gratified to find myself in such close agreement with the listing of important developments compiled by one with an outlook so different from mine. There is also good material in Vance's chapter on American demography. The biologist will miss little if he skips the rest of Parts I and II.

The most significant point emerging from Part III is that the data of demography are downright inadequate. The chapters by Hawley and by Dorn make this point succinctly and in much less anesthetic prose than others of the chapters numbered 15-25.

Ackerman's two chapters dealing with "natural resources" and "geography" are well worth reading. In Part IV, Peter Frank's chapter on "Ecology and Demography" is the only really biologically oriented chapter in the book and may be the most interesting to readers of Ecology. Its purpose, however, is not so much to inform ecologists as to tell sociologists about us. Also in Part IV, Spuhler does as nice a job as I have seen of explaining the elements of population genetics in a simple and interesting way.

This book is dull not just because of the unevenness characteristic of symposia but also because it is replete with repetition, circumlocution, and solemn pronouncements of utter trivia phrased in involved language. The first two chapters read like two drafts of the same contribution. Terms like "normative," "nexus," "frame of reference," "referents," "substantive," "spaciotemporal," and "socioeconomic" appear often enough to fill a number of pages if they were all brought together. We are repeatedly reassured that demography is a science (with a frame of reference), that it is not a biological but a social science (contraception is an "applied science," p. 421), and that it is not properly appreciated.

Certainly, many of the authors have not sought the appreciation of readers who like simple things to be said simply. It is asking a lot to expect the reader to flip pages back and forth so that he can translate statements like (p. 798) "Because of the superiority of data gathered by (d) and (iv) methods to data gathered by (a) and (i) methods, it is likely that the relative importance of (d) and (iv) methods will increase." It is somewhat easier to understand that (p. 414, cf. p. 419): "Necessary but not sufficient conditions for fertility are coitus (except for artificial insemination) and fecundity." Who can doubt (p. 410) that a "source of the fall in fertility was a decline in the mean completed parity of married women . . ." ? or that (p. 418) there is "a concentration of low fecundity women in the low parities"? On p. 398 we are informed that "Variations in fertility among the population are greater than variations in mortality."—a later author (p. 563) puts this more succinctly: "Everybody dies, once and no more often."

Can it be that some sociologists actually think in such terms and so must conduct studies to discover the obvious? Consider the following (p. 495): "One almost universal finding from these data is that the volume of gross migration (in-migration plus out-migration) for a community is much greater than the net migration." If we put this in formal terms, letting a and b represent two numbers greater than zero standing for in- and out-migration, then the statement tells us that $a + b > a - b$, which is equivalent to saying that $2 > 0$. Many comparable examples could be exhibited!

I once heard a prominent geographer say that his was a dying field because biologists beat the geographers to the development of ecology. Can it be that the sociologist "demographers" are apprehensive of biological intrusion? Why do so many of these authors ignore biology (and biologists; Kinsey is not even mentioned!)? It seems rather pointed (p. 573) to tell prospective demographers that "knowledge in one or several diverse fields, such as mathematics, statistics, economics, sociology, medicine, anthropology, and history, can be of great value."

I have said it before and I still believe that demography should be considered a branch of biology. Certainly, the cultural and social influences are important, but the latter at least is important also in populations of other vertebrates and insects. I am confident that we must understand the features common to biological populations in general before we shall be prepared to understand the peculiarities characterizing a particular species. The great generalizations of physics and chemistry were not achieved by studying the behavior of individual particles; in fact it might have confused Boyle if he could have watched the eccentric behavior of individual molecules.

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[1] Hauser, Philip M. and Otis Dudley Duncan (editors). 1959. The study of population; an inventory and appraisal. (symposium) University of Chicago Press, Chicago; University of Toronto Press, Toronto. xvi + 864 pp., 15 figs., 75 tables. $15.00.

There is at least a danger that too much concern with such features as urbanization and the motivation of couples for fertility control may obscure the operation of larger processes.

Finally, I should comment on Duncan's chapter on "Human Ecology" since I have never before been able to understand the subject matter of that field. It wasn't easy this time, but information theory tells us that reception is possible even over a very noisy circuit if the message is sufficiently redundant; and after several readings he began to get through to me. Happily, it appears that there is after all a connection between "human ecology" and "the ecology of man" although "human ecologists" appear to be interested in only a limited portion of the synecology of man.

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THE MAMMALS OF NORTH AMERICA[1]

Hall and Kelson dedicate their monolithic work to Linnaeus and Spencer Fullerton Baird. The publisher cites the work of the latter two as being the ". . . only two contributions which may be compared with this . . ." new publication, hence ". . . the first work of its kind in 100 years." Without discussion of the validity of this advertising, it is of interest to note the establishment of a well-worked field of mammalogy on this continent over the past century by comparing numbers of genera and species listed in the Mammals of North America of 1859 and of 1959: Rough counts by this reviewer show 57 genera and 253 species listed by Baird and, for a comparable geographic unit (United States exclusive of Alaska and Hawaii), Hall and Kelson list 99 genera and 409 species. It is in the extremes of this continent, of course, that the most dramatic modern expansions of our knowledge of faunistic mammalogy have occurred: Of the 236 genera and approximately 938 species treated by Hall and Kelson, 160 genera and 503 species occur south of the United States—Mexico, Central America, and the West Indies—thus a majority!

The very magnitude of information now available on the subject would, perhaps, permit in the future similar publications restricted to individual topics concerning the mammals of this continent, such as an *Ecology of . . .*, a *Reproductive Physiology of . . .*, etc., deriving considerable aid from this present compilation of taxonomic and range information. At any rate the authors were faced with a task of some magnitude in selecting pertinent characteristics of each taxon above the subspecies level. The resulting summary draws from such varied subjects as food habits, habitat selection, economic status, litter size, gestation period, longevity, and activity, as well as a more complete and detailed description of the taxonomic characterizations utilizing skull, external body features, and distribution. Where the former features do not receive uniform mention, the authors were generally met with deficiencies in the literature.

Although characterizations and keys to the different taxa constitute the bulk of the two volumes, there are two general sections: an excellent "Suggestions for collecting and preparing study specimens of mammals" and a 7½-page introduction to the zoogeography of North American mammals.

The recency of the coverage of literature is good for a work of this size: ". . . all pertinent taxonomic and distributional information that came to our attention up to October 31, 1957," with addenda that include literature citations as recent as 1958. The history of the writing of the bulk of different taxonomic sections of the book will be apparent to those following the University of Kansas Museum of Zoology publication series from 1945. For example, Lagomorpha is a republication of "A Synopsis of the North American Lagomorpha" (E. R. Hall, 1951, UNIV. KANS. PUBL. MUS. NAT. HIST., 5(10): 119-202) with recent distributional information inserted in the text and in the addenda. The authors have conscientiously modified maps and textual material from this publication series as new information appeared in the literature.

The taxonomic judgment of the authors is, as would be expected, technically sound and sufficiently conservative to be an accurate presentation of the literature of the North American workers on this subject, to which Dr. Hall and his students have contributed no small amount. This judgment, as that of any student concerned with a faunistic area, should reflect the status of knowledge of the groups beyond merely the area of concern, even though this area may be an entire continent. The modern trend toward single holarctic species is accepted where the authors consider there is evidence for intergradation between continents, as in the moose, *Alces alces,* and the caribou-reindeer, *Rangifer tarandus.* The question of single species is raised but not answered affirmatively on the grounds of present lack of evidence for the wapiti, *Cervus canadensis,* and the red deer, *C. elaphus,* and the red foxes, *Vulpes fulva* and *V. vulpes.* In a few cases considered by European workers, this question is not mentioned by the authors: in the northern wild cats, *Felis lynx* and *Lynx* species, and in the large brown bear and grizzly bears, *Ursus arctos* as opposed to *U. absarokus, alascensis, alexandrae, andersoni,* and so *ad infinitum* or at least through the 78 species of North American brown and grizzly bears. The latter instance is regrettable, both from the standpoint of failure on the part of North American mammalogists to revaluate the awkward heritage of C. Hart Merriam's taxonomy of Ursidae and from the standpoint of Hall and Kelson's failure even to mention the views of certain European workers on *Ursus arctos* in North America. In this regard Erbrink's A REVIEW OF FOSSIL AND RECENT BEARS OF THE OLD WORLD (1953, Deventer-Drukkerij Jan de Lange) and J. R. Ellerman and T. C. S. Morrison-Scott's CHECKLIST OF PALAEARCTIC AND INDIAN MAMMALS 1758 TO 1946 (1951, British Museum (Nat. Hist.)) are not acknowledged. Couturier's L'OURS BRUN (1954) is cited as the revision of Eurasian big brown bears without mention of his views on this subject. In view of Dr. Hall's extremely conservative resistance to consolidation under the single species, *Ursus arctos,* presumedly on the grounds that no intergradation has been shown between Eurasia and North America (as well as failure of European workers to examine Merriam's types), it is surprising to find his acceptance of *Ursus arctos* on St. Lawrence Island.

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[1] Hall, E. Raymond and Keith R. Kelson. 1959. The mammals of North America. The Ronald Press, New York. 2 Vols., 1083 pp., with an additional 158 pages of indices to vernacular and technical names. $35.00.

The format is attractive and follows the general pattern as well as the level of excellence established by Dr. Hall and his group of students and associates in the University of Kansas publications of the Museum of Natural History. The distribution maps for each species, with current subspecies, are clear and quickly interpreted except for species with large numbers of subspecies concentrated in small geographic areas. This could have been corrected by arranging the numerical legend for subspecies in a logical geographical order. Pen and ink sketches by C. G. Pritchard, R. P. Grossenheider, and other artists add greatly to the understanding of less known forms, particularly from Central America. The original outline drawings of the skulls are noteworthy contributions. The keys within each order to family, to genus, and to species are paginated to the textual description and are easily followed.

The student acquainted with mammals only at a popular field-guide level and the professional biologist will both find this book usable because of the clarity of presentation of material. The former will find information on collection, recognition, distribution and, for the better known species and genera, considerable information on natural history. The latter will also certainly benefit from the characterization of taxa, the summary of literature with its inherent indications of areas of inadequacy of knowledge, and the general reference utility of this authoritative treatment of the mammals of the New World from the Arctic to Panama.

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A MANUAL OF VERTEBRATES[1]

The primary objective of this book, as set forth by the authors, is to present a complete, annotated list of all known vertebrates of the United States. In this way the volume is to replace the old vertebrate manuals of Pratt and Jordan. In its nomenclatural inclusiveness the objectives are fulfilled, except for the rather unfortunate omission in some sections of well-established species. For example, Moore does not include the common killifishes of the eastern seaboard, *Fundulus majalis* and *F. similis*, that commonly are taken with other included species. In addition, Parkes (WILSON BULL., vol. 70, no. 1, pp. 101-104, 1958) has commented that had the "northern limit not been set at the artificial border between Canada and the United States," the book would have gained much in usefulness while incorporating but a handful of additional species.

The book's five systematic sections have been reviewed previously by Hecht (COPEIA pp. 60-61, 1958), Parkes (*ibid*) and Manville (JOUR. MAMMALOGY, 39: 159-160, 1958). Moore's section on the fishes has hitherto received only brief or indirect comment. Although excellent from the standpoint of taxonomic arrangement, this section is marred by inconsistencies and peripheral errors of annotation (see also Hecht, *ibid.*). Size, color patterns, and other identifying characters frequently are omitted and the sequence of characters transposed, ranges are not always clearly stated, and in still other places trivial characters only are mentioned, thus giving them an aura of undeserved significance.

In a work of this kind figures are indispensable, yet of the meagre few that are presented their quality is poor, and details of the figures do not correspond with accompanying text description, e.g. on page 130, fig. 2-72, scale counts of *Notropis signipinnis*. If the fish section had been extended to cover territories north of the United States, as suggested by Parkes, it would have been necessary to include only another 25 or so species.

As a compendium, the book has immense value, however. Its practical value for students and teachers is demonstrable when used in conjunction with more detailed and comprehensive field guides and keys to regional faunas.

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[1] Blair, W. Frank, Albert P. Blair, Pierce Brodkorb, Fred R. Cagle, and George A. Moore. 1957. Vertebrates of the United States. McGraw Hill Book Company, New York, London, Toronto. ix + 819 pp., 444 figs., taxonomic keys. $12.00.

TEXTBOOK OF ORNITHOLOGY[1]

The senior author of this textbook had a long and illustrious career in museum research, and as author, editor, and teacher. He served as president of the American Ornithologists' Union and of the Wilson Ornithological Society and nine years as editor of the WILSON BULLETIN. At the time of his death on January 30, 1957, he was Curator of Birds in the University of Michigan Museum of Zoology and Professor of Zoology. The junior author received his Ph.D. in 1950 from the University of Michigan and is now Associate Professor of Anatomy in the University of Michigan Medical School.

The book has been long in preparation. At the time of his death Van Tyne had 4 chapters largely completed, including the long synopsis of bird families, and had partially written 2 others. Berger is responsible for writing 7 chapters based largely on Van Tyne's lecture notes and bibliographical cards and for putting the entire book in final form.

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[1] Van Tyne, Josselyn and Andrew J. Berger. 1959. Fundamentals of ornithology. John Wiley & Sons, Inc., New York; Chapman & Hall Ltd., London. xi + 624 pp., 253 figs. $11.75.

The longest chapter, making up nearly one-third of the book, deals with the classification of the birds of the world by families. This is a very useful reference source and is the most valuable feature of the book. For each family are given physical characteristics, range, habits, food, breeding, technical diagnosis, classification, references, and synonymy, as well as a pen and ink drawing of a representative species by George M. Sutton. "Technical diagnosis" and "classification" are covered by citations only, but otherwise much information is packed into brief statements on each topic. Consistency is carried *ad absurdum,* however, in devoting one full page to each family, regardless of whether it contains 1 species or 398, and in citing approximately the same number of "references" for each family.

The other 12 chapters furnish a general introduction to the subject matter of ornithology. The discussions are biased toward anatomy, classification, and terminology and are weak on functional explanations, ecology, and the dynamic approach. There is a long, valuable glossary of terms and extensive references at the end of the chapters.

A chapter of special ecological interest, "Bird Distribution," begins with a rough, partly out-of-date map of zoogeographical regions, and there is a list of families found in each. The origins of the North American avifauna are also listed. Life-zones, biomes, and biotic provinces are briefly referred to, but without much evaluation or discussion of their usefulness. Differences in the ranges of birds are illustrated, and factors controlling distribution are discussed in a general manner. The entire chapter, with references, includes 26 pages. Other chapters cover, in a similar cursory manner, paleontology, anatomy, plumage and molt, senses and behavior, voice and sound production, migration, flight, food and feeding habits, breeding behavior, social relations, and taxonomy and nomenclature. Missing is any adequate discussion of evolution and phylogeny, comparative behavior, conservation, ecology, and study methods. Bird-banding, for instance, is not even listed in the Index.

The book is not comprehensive in its coverage and leaves much to be desired as a textbook for college classes. The long chapter on bird families is not of much interest to beginning students, the other 12 chapters are too elementary for advanced students. In general, however, the book is reliable and authoritative as far as it goes.

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Wild Vertebrates and Man in Sweden[1]

This book describes the wild vertebrates in their natural habitats in Sweden. The invasion of these animals into Sweden beginning with the melting of the glacial ice about 15,000 years ago, and their fate since that time, are briefly described. The animal and plant life, climatic conditions, geological events, and cultural periods since that time are presented in tabular form. Emphasis, in 12 of the 15 chapters, is placed upon the relationships between the animals, the environment, and man. Adaptations of animals to man's activities are pointed out. The animal life, and more briefly the plant life, are described according to physiographic regions, such as oceans and coasts, plains and fields, hardwood forests, coniferous forests, lakes and marshes, bogs, and the alpine region. The numerous photographs (not numbered) usually show the animals in their natural habitats. The index of Swedish common names contains the scientific names of all the vertebrates that are discussed. This is an excellent book for both the ecologist and the amateur.

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[1] Curry-Lindahl, Kai. 1955. Djuren och Människan i Svensk Natur. Lars Hökerbergs Bokförlag, Stockholm. 463 pp., numerous figs. Kr. paper 28:50, cloth 34:50 ($5.50, 6.60).

The Biology of Brackish Water[1]

This twenty-second volume, in the well known series on limnology originated by August Thienemann in 1925, deals with the physical characteristics and life of somewhat salty waters. Such waters have been a scientific *mare incognita* for limnologists and oceanographers; neither group wishing to work in an "atypical" situation. On the other hand, investigators at marine laboratories, particularly physiologists, have had a field day. Thus the purely biological aspects, without especial reference to all environmental conditions, have been emphasized in modern research and this book faithfully records that impression.

The two authors have written entirely separate parts of the volume. Professor Remane handles the ecological aspects and Professor Schlieper the physiological. Unfortunately, this arrangement includes separate bibliographies with some redundancy. The indices are unified, however. These include an author index, a completely inadequate subject index, and an index to genera. The authors rather apparently feel that information on par-

[1] Remane, A. and C. Schlieper. 1958. Die Biologie des Brackwassers. Vol. 22 in: Die Binnengewässer, ed. by A. Thienemann. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. 348 pp., 139 figs., 43 tables. DM 58.—, $14.66.

ticular organisms is of greater interest than that on general concepts and phenomena.

The ecological section is divided into five major divisions: definitions, origins and hydrography of brackish water; the special features of organisms adapted to brackish water; the types of brackish water organisms and their salinity tolerances; life zones in relation to substrate; and a discussion of some typical brackish water areas with the emphasis on the Baltic and the Black Sea-Caspian Sea region. This last part touches on a variety of habitats including lakes, river mouths, ponds and coastal ground water.

Professor Remane stresses zoogeography; but there is some botanical data included, referring both to plants as substrates and to their responses to salinity. There is not, however, any reference to dynamical ecology, inter- and intraspecies competition, food chains, prey-predator energetics and the like. Neverthless, as far as it goes, this section is a thorough, well-documented exposition. It should provide an immense resource of information on the distribution and abundance of organisms in a severely limiting environment. It will be less useful to those interested in community interaction and energetics.

Professor Schlieper's contribution on the physiological responses of animals (and in a few cases, plants) to steady and varying salinity conditions is an excellent summary of recent literature. Ion regulation, volume regulation, respiration, resistance to extreme temperature, integument permeability and chemical composition, all in relation to salinity conditions, are some of the subjects Schlieper discusses. The approach is strictly physiological with no hint of the biochemical mechanisms involved.

The volume is well printed and well bound. Typographical errors are rare. The comparatively high price would seem to be a result of substantial royalties rather than production costs.

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APPLIED HUMAN ECOLOGY[1]

Even more than in many other fields some of the documents of interest to ecology appear under titles and auspices not immediately referable to ecology. Such a paper is reviewed here. It is frankly propaganda, but of a constructive sort, propaganda against the desecration of the Potomac Valley. Focussed at first on the Chesapeake and Ohio Canal as a central feature of the valley, it broadens out to discuss, in an environmental and social context, outdoor recreation, highways, dams, water supply and pollution, economic development, and social organization in the valley. It brings out the characteristics of this region as an environment for man. It exposes the weaknesses and fallacies inherent in much of the present piecemeal planning proposed to meet the current congestion and population expansion. It suggests what seem to be very tenable and acceptable alternatives to big dams and super-highway networks, and it extolls the values, in terms of health and happiness, of preserving the opportunity for outdoor life and small-community social patterns. It warns effectively of the consequences of unrestrained population growth. Its tone in general suggests not that we refrain from carrying on the normal and desirable activities of a modern community, but that we carry them on in an intelligent manner, with awareness of the nature of our environment and with deliberate planning for its preservation. Means are proposed to utilize the resources of the valley and to assure at the same time a sustained productivity and an independent democratic culture.

The paper is scarcely organized as a conventional ecological paper would be, though the relations between man and his environment are constantly stressed. It is conservation oriented, and, insofar as we recognize that conservation is one of the great branches of applied human ecology, this work is of interest to ecology. Certainly one of the great tasks of ecology is to develop the knowledge and understanding necessary for the continued maintenance of a suitable habitat for man. This booklet is a valuable step toward carrying out this task.

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[1] Smith, Anthony Wayne, *et al.* 1959. Outline program for the use and enjoyment of the Potomac Valley. Citizens Committee on Natural Resources, Washington. 48 pp., 8 photos.

A PHYTOSOCIOLOGIST'S STUDY OF EPIPHYTE COMMUNITIES[1]

The phytosociology of epiphytic cryptogams has claimed the attention of a surprisingly large number of taxonomists and ecologists in Europe, North America, and Japan. These innumerable studies, published in a wide variety of langauges and journals, have finally been summarized and integrated in a large volume which will undeniably be the standard reference work for years to come. It represents more than ten years of concentrated effort by the Dutch botanist J. J. Barkman, a well-known bryologist and ecologist, in investigating first-hand the cryptogamic associations of north-central Europe and assembling and evaluating nearly all the pertinent literature. The text is written lucidly in English, with a minimum of emphasis on special terminology, reflecting credit on the author and the publisher.

The first half of this book, 340 pages with a bibliography of about 500 references, is really a textbook. Except for only moderate coverage of recent Japanese work, Barkman has done a remarkably complete and objective job of summarizing the classical, largely descriptive subject matter of epiphytic cryptogams. There are four main chapters. Chapter II (Ecology) covers in detail the environmental factors affecting the distribution of cryptogams, with especially full discussions of water relations and chemical factors. Chapter III (Composition, structure, and dynamics of epiphytic vegetation) and Chapter IV (Chorology) contain a standard summary of growth forms, succession, dispersal, etc. Chapter V (Synsystematics) is an interesting and enlightening discussion of the methods used in sampling and naming the associations. The second half of the book, with the accompanying supplement of loose tables, is taken up by a detailed inventory of 98 associations of epiphytic communities recognized by Barkman in the Netherlands, arranged according to the format and nomenclature of the Montpellier or Braun-Blanquet school.

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[1] Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes, including a taxonomic survey and description of their vegetation units in Europe. Van Gorcum & Co., Assen, Netherlands. xiii + 628 pp., 20 figs., 50 maps, 16 plates & supplement of tables on 35 loose pages. Hfl. 44.00, $11.60.

The theoretical foundations of this text are obviously drawn from the large body of European work since 1900 that has dominated the field of cryptogamic sociology. It cannot be expected that the relatively recent studies using a statistical approach would significantly alter Barkman's viewpoint. However, I cannot avoid criticising certain aspects of the European methodology insofar as data derived from it are used to establish a theoretical basis for the science. The main, often voiced criticism of the Braun-Blanquet school is that the sampling methods are based on subjective criteria. For example, Barkman explicitly states (p. 300) that "only trees with a well-developed homogeneous epiphytic vegetation were studied" in connection with his research on associations in the Netherlands. How did Barkman know that the vegetation was homogeneous? In my estimation, such a subjective criterion for selecting samples will give us valid data *only* for the most typical vegetation, and every ecologist will differ in some degree in his judgment of the most typical vegetation. Barkman himself admits that the voluminous data in European papers are usually not comparable because of the lack of a uniform sampling method.

I do not believe that any field work based on the so-called "sociologischen Blick" can give us even such fundamental data as the frequency of a cryptogam on a certain species of tree, much less the frequency in the vegetation. Without a common denominator, such as a random sampling technique provides, cryptogamic sociology will remain a subjective, descriptive science, each association of cryptogams representing the personal opinion of a single ecologist. The Europeans seem to fear that a statistical (or better a random sampling) method will destroy their hierarchy of associations. Yet the quantitative work done by Americans, which is reproducible by any ecologist, has shown that there may be statistically distinct combinations of species or communities, a point which Barkman missed completely. On the other hand, Barkman drew heavily, if not exclusively, on American work to present unbiased figures on the frequency of cryptogams in various forest types, on different tree species, and on the same trees, and the average number of species per tree. Comparable data cannot be derived from the elaborate tables which Barkman prepared.

Phytosociology must eventually be reduced to a quantitative basis, if the science is going to advance with other fields of knowledge. Fortunately cryptogams are probably more adaptable to such a technique than any other plant group, because of the lesser number of species, the relative homogeneity of the vegetation, and the restricted habitats. With a quantitative concept, data regarding cryptogams can be transformed into numbers which can be analysed by computing machines to provide unbiased data (within the limits of error of the sampling methods) understandable and reproducible by ecologists in every country. At the same time, there will always be some need for the current descriptive methods, in particular at the popular level, and for this reason Barkman's book will remain as the main reference for qualitative sociology of epiphytic cryptogams.

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A Vegetation Bibliography for the Northeastern States[1]

Not only review editors with books overflowing their offices, but all who strive to keep up with and keep track of the ecological literature are aware of the difficulty of doing so. One cannot both read what appears, and prepare cards to keep a record of and later relocate what one has seen, without the deflection to this purpose of much time needed for research or other purposes. The individual scholar who has invested this time, and can make the benefits available to others, may deserve their appreciation.

A vegetation bibliography of the Americas has been a long-term project of Frank E. Egler, from which three state bibliographies appeared earlier (Connecticut, Rhode Island, and Massachusetts, Phytologia 3(1): 1-26, 1948, 3(2): 49-56, 1949; 3(5): 193-237, 1950). The present list covers the literature through 1958 for these three states and six additional ones—New York, New Jersey, and Pennsylvania, and Maine, Vermont, and New Hampshire—and is intended to be the first of a series of such regional bibliographies. For each state there is an outline map showing location of vegetation studies included. These localities appear in alphabetic order in the bibliography, with papers describing their vegetation in chronological order under the locality. Each reference is briefly described or characterized. The list is not intended to be a complete bibliography; it is a selection of papers regarded by the author as of significant usefulness to those concerned with plant communities and vegetational geography. It thus represents a choice by the author of one of the two major alternatives of vegetation bibliography: a complete listing, which is likely to run to hundreds of titles and must generally be unannotated, and a selective, annotated list. Each of these has its different usefulness; but the latter may have the broader value in offering direct guidance to papers of most value, rather than a long list which the reader must work through for himself.

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[1] Egler, Frank E. 1959. A cartographic guide to selected regional vegetation literature—where plant communities have been described. Sarracenia, No. 1, 50 pp., 9 maps. Available from Institut Botanique de l'Université de Montréal, 4101 est, rue Sherbrooke, Montréal 36.

The author observes that there are omissions from his list, which should be called to his attention for future revision. Apart from the lists of papers, the reviewer noted the absence of reference to the accounts in E. Lucy Braun's DECIDUOUS FORESTS OF EASTERN NORTH AMERICA, or to the NATURALIST'S GUIDE TO THE AMERICAS as a source of information on study areas and limited material on state vegetation. Although the arrangement of papers is a useful one, there is no table of contents or index. Entry of counties on the maps might increase their usefulness, but would also make less evident one of the significant features of these maps—the very wide scattering of areas in which vegetation has been studied, the broad gaps in knowledge of vegetation in this longest and most densely occupied part of the country.

The author states that his lists are intended primarily for those who are not authorities in vegetation science, or for the individual areas included. The first of these restrictions might seem to understate the value of such a list for professional ecologists. The ecologist or non-ecologist who wants to know what is available on the vegetation of a particular area should find the list a most helpful means of locating the more significant vegetation studies, the literature he will want to consult first.

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BOOKS AND MONOGRAPHS RECEIVED FOR REVIEW

Anfinson, Christian B. 1959. The molecular basis of evolution. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. xviii + 228 pp., 99 figs., 17 tables. $7.00.

Bailey, Norman T. J. 1959. Statistical methods in biology. John Wiley & Sons, Inc., New York. ix + 200 pp., 33 tables. $4.50.

Baldwin, W. K. W. 1958. Plants of the Clay Belt of northern Ontario and Quebec. Canada Department of Northern Affairs and National Resources, National Museum of Canada Bulletin No. **156** (Biological Series No. 55), vi + 324 pp., 17 plates, 4 maps, 11 tables. $2.00.

Bellrose, Frank C. 1959. Lead poisoning as a mortality factor in waterfowl populations. Ilinois Natural History Survey, Urbana, Bulletin, Vol. **27**, Art. 3, pp. 232-288, 9 figs., 31 tables. $0.50.

Bertalanffy, Ludwig von and Anatol Rapoport (editors). 1957. General Systems: Yearbook of the Society for General Systems Research, Vol. **2**. (symposium) xiii + 188 pp., figs. $7.50.

Bertalanffy, Ludwig von and Anatol Rapoport (editors). 1958. General Systems: Yearbook of the Society for General Systems Research, Vol. 3. (symposium) xxiii + 259 pp., figs. $7.50. Mental Health Research Institute, University of Michigan, Ann Arbor.

Campbell, Frank L. (editor). 1959. Physiology of insect development. (symposium) Univ. Chicago Press, Chicago; Cambridge Univ. Press, London; Toronto Univ. Press, Toronto. xiv + 167 pp., 13 figs. $4.00.

Clark, Wilfrid E. Le Gros, and others. 1959. Commemoration of the centennial of the publication of *The Origin of Species* by Charles Darwin. (symposium) Proceedings of the American Philosophical Society, Vol. **103**, No. 2, pp. 159-319. $1.00.

Cowles, Raymond B. 1959. Zulu journal; field notes of a naturalist in South Africa. University of California Press, Berkeley & Los Angeles. xiv + 267 pp., 32 plates. $6.00.

***Curtis, John T.** 1959. The vegetation of Wisconsin; an ordination of plant communities. University of Wisconsin Press, Madison. xi + 657 pp., 66 plates, num. tables & figs. $7.50.

Davis, Kenneth P. 1959. Forest fire; control and use (with chapters by George M. Bryam and W. R. Krumm). McGraw-Hill Book Co., Inc., New York, Toronto, London. xiii + 584 pp., figs. & tables. $12.00.

Dougherty, Ellsworth C. (editor). 1959. Axenic culture of invertebrate metazoa: a goal. (symposium) Annals of the New York Academy of Sciences, Vol. **77**, Art. 2, pp. 25-406. $4.50.

Dowdeswell, W. H. 1959. Practical animal ecology. Methuen and Co. Ltd., London. 316 pp., 86 figs., 21 tables. 32s 6d, $4.60.

Edmondson, W. T. (editor). 1959. Fresh-water biology (Ward and Whipple). (symposium) 2nd ed. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. xx + 1248 pp., num. figs., taxonomic keys. $34.50.

Eibl-Eibesfeldt, Irenäus. 1959. Survey on the Galapagos Islands. UNESCO, Paris, Mission Reports no. **8**. 31 pp., 60 figs. Columbia Univ. Press, New York. $0.75.

Free, John B. and Colin G. Butler. 1959. Bumblebees (with two appendices by Ian H. H. Yarrow). The Macmillan Co., New York (The New Naturalist Series): Collins, London. xiv + 208 pp., 3 figs., 24 plates. $5.00.

***Gaussen, Henri.** 1954. Géographie des plantes. Librairie Armand Colin, Paris. 224 pp.

Gebhardt, Louis P. and Dean A. Anderson. 1959. Microbiology. 2nd ed. C. V. Mosby Co., St. Louis. 476 pp., 69 figs., 22 tables. $5.75.

Gorbman, Aubrey (editor). 1959. Comparative endocrinology. Proceedings of the Columbia University Symposium on Comparative Endrocrinology, held at Cold Spring Harbor, New York, May 25 to 29, 1958. John Wiley & Sons, Inc., New York; Chapman & Hall, Ltd., London. xx + 746 pp., figs. $15.00

Harlow, William M. 1959. Fruit and twig key to trees and shrubs—fruit key to northeastern trees, twig key to the deciduous woody plants of eastern North America. Dover Publications, Inc., New York. 50 & 56 pp., figs. & taxonomic keys. $1.25.

Hayward, C. Lynn, D. Elden Beck, and Wilmer W. Tanner. 1958. Zoology of the Upper Colorado River Basin. I. The biotic communities. Brigham Young University Science Bulletin, Biological Series, Vol. **1**, no. 3, 74 pp., 21 figs., 3 tables.

Hirschfield, Henry I. (editor). 1958. The biology of the Amoeba. (symposium) Annals of the New York Academy of Sciences, Vol. **78,** Art. 2, pp. 401-704, figs. $4.50.

Horsfall, J. G. and A. E. Dimond (editors). 1959. Plant pathology; an advanced treatise. Vol. **1.** The diseased plant. (symposium) Academic Press, New York & London. xiv + 674 pp., figs. $22.00.

International Urban Research. 1959. The world's metropolitan areas. University of California Press, Berkeley and Los Angeles. ix + 115 pp., tables. $3.00.

***Keast, A., R. L. Crocker, and C. S. Christian** (editors). 1959. Biogeography and ecology in Australia. (symposium) Dr. W. Junk, The Hague (Monographiae Biologicae Vol. **8**). iv + 640 pp., 56 figs., 18 plates. Hfl. 65.—, $15.20.

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CORRECTION

In the paper "Interpretation of loop-frequency data as a measure of plant cover" by S. S. Hutchings and R. C. Holmgren, Ecology 40 (4), 1959, on p. 671, the last 3 lines of the legend for Fig. 2 should read "area for given numbers of plants (N), per square foot. Curves are for theoretical populations of circular plants of uniform size."